ARTHROPOD COMMUNITIES AND PASSERINE DIET:

EFFECTS OF SHRUB EXPANSION IN WESTERN ALASKA

By

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ABSTRACT

Across the Arctic, taller woody shrubs, particularly willow (*Salix* spp.), birch (*Betula* spp.), and alder (*Alnus* spp.), have been expanding rapidly onto tundra. Changes in vegetation structure can alter the physical habitat structure, thermal environment, and food available to arthropods, which play an important role in the structure and functioning of Arctic ecosystems. Not only do they provide key ecosystem services such as pollination and nutrient cycling, they are an essential food source for migratory birds. In this study I examined the relationships between the abundance, diversity, and community composition of arthropods and the height and cover of several shrub species across a tundra–shrub gradient in northwestern Alaska. To characterize nestling diet of common passerines that occupy this gradient, I used next-generation sequencing of fecal matter. Willow cover was strongly and consistently associated with abundance and biomass of arthropods and significant shifts in arthropod community composition and diversity. Key nestling prey items were positively associated with both willow and ericaceous shrubs. Diet composition varied significantly among bird species and spatially within species, however, I found that temporal variability in prey abundance did not have a strong relationship to the probability of consumption. I predict that the wide temporal window of prey availability and high diet diversity may protect these birds against negative impacts from climate-driven shifts in prey phenology and abundance. Taken together, my results suggest that shrub expansion could result in a significant shift in Arctic food-web structure and an increase in food availability for insectivores, although future ecosystem change in the Arctic is likely to be heterogeneous as shrub types are expanding at different rates and in different places across the Arctic.

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CHAPTER 1. GENERAL INTRODUCTION

Tall, deciduous shrubs have increased in cover and height across the Arctic in recent decades (Sturm et al. 2001, Tape et al. 2006) due to permafrost thaw, warmer spring temperatures, increased fire frequency, and disturbance (Racine et al. 2004, Myers-Smith et al. 2011, Elmendorf et al. 2012, Lantz et al. 2012). Shrub expansion has been linked with changes in the distribution and abundance of moose (*Alces alces)*, snowshoe hares (*Lepus americanus*), and ptarmigan (*Lagopus lagopus*) in the Arctic and Subarctic (Christie et al. 2015, Tape et al. 2016); however, we have little specific knowledge about how such large-scale vegetation changes will affect arthropods or the migratory birds that depend on them for food. In this thesis I sampled arthropod communities across a tundra-shrub ecotone to quantify arthropod distribution, abundance, and diversity relative to shrub characteristics. To examine trophic relationships between arthropod prey and insectivorous passerines, I also used next-generation sequencing to characterize the nestling diet of 5 migratory songbirds. From these data, I then assessed diet diversity and drivers of variation in diet composition.

Shrub expansion encompasses three phenomena: 1) an increase in shrub height, 2) in-filling of existing shrub patches, and 3) colonization of previously non-shrub habitats (Tape et al. 2006, Myers-Smith et al. 2011). Alder (*Alnus* spp.), willow (*Salix* spp.), and birch (*Betula* spp.) are the species most responsible for shrub expansion in the Arctic, although there are substantial regional differences in the relative increase of these shrubs. For example, willow is the most rapidly increasing shrub in western Canada and northern Russia, whereas alder and birch are increasing more rapidly in Alaska (Bret-Harte et al. 2001, Myers-Smith et al. 2011, Elmendorf et al. 2012). These changes alter the habitat available for other species by increasing deciduous canopy cover and plant height, decreasing plant diversity, and decreasing the area of neighboring

tundra habitats (Myers-Smith et al. 2011). Increased shrub cover and height may also change abiotic factors important to animal communities such as solar radiation, soil moisture, soil temperature, and snow cover by providing shade in summer and accumulating snow in winter (Lantz et al. 2012, Sweet et al. 2014, Hansen et al. 2016).

Changes in plant species composition and thermal conditions resulting from an increase in deciduous shrub dominance are expected to exert a large influence on arthropod communities, which are a major component of Arctic biodiversity (Meltofte et al. 2013) and provide essential ecosystem services such as pollination and nutrient cycling (Triplehorn and Johnson 2005, Hodkinson et al. 2013). Arthropods, as the most diverse animal phylum, occupy all trophic levels of Arctic food webs (Hodkinson and Coulson 2004) and should therefore respond in diverse ways to environmental and vegetation change (Hodkinson and Bird 1998).

There is evidence to support the idea that not all groups of arthropods respond similarly to shrub dominance. Recent studies on Alaska's North Slope found that shrub thickets supported a greater abundance and biomass of flies (Diptera), parasitic wasps (Hymenoptera), and herbivorous bugs (Hemiptera), but a lower abundance and biomass of spiders (Araneae) (Rich et al. 2013). Such numerical differences among taxonomic groups can result from variation in the species' physiology, nutritional demands, and preferred habitat. Increased shade in shrub patches may create an unfavorable thermal niche for ground-dwellers such as wolf spiders (Araneae: Lycosidae) and ground beetles (Coleoptera: Carabidae), whose activity is strongly influenced by direct sunlight (Hoye and Forchhammer 2008). The community of flowering plants is altered in shrub thickets by inclusion of more shade-tolerant forbs but fewer ericaceous species; such changes in plant composition may be less favorable for some pollinators but benefit others (Swanson et al. 1985, Pajunen et al. 2012). Increased soil moisture and leaf litter found in shrub

thickets may create more favorable conditions for springtails (Collembola), centipedes (Chilopoda), snails (Gastropoda), and worms (Annelida) (Hodkinson et al. 2013), which lack the waxy cuticle of spiders and insects and are sensitive to desiccation (Triplehorn and Johnson 2005). Arctic shrub thickets have greater overall plant biomass, leaf area, and leaf biomass than tundra vegetation (Shaver and Chapin 1991, Tape et al. 2006), thus providing more resources to support greater abundances of herbivorous insects. Increased abundance of herbivorous insects may in turn change the abundance of predator and parasitoid species that feed on them (Wirta et al. 2015).

Shrub thickets accumulate snow in winter and delay snowmelt in spring by shading snow patches (Lantz et al. 2012). The effects of snow accumulation are complex and vary among arthropod taxa. Snowpack in winter provides insulation from extreme temperatures, but later snowmelt in spring delays development and effectively shortens the time arthropods have in which to complete their life cycles. Some springtails and spiders stay active beneath the snow layer (Hagvar 2010), and chironomid midges (Diptera: Chironomidae) can emerge early from snow patches (Braz et al. 2014), suggesting these groups may be less negatively affected by delayed snowmelt than other arthropods that are fully dormant under snow. This idea was supported for spiders by a snow-fence experiment that showed no effect of accumulated snow on community composition or phenology (Legault and Weis 2013). Large, late-melting snow patches shaded by shrub thickets may be beneficial for taxa with aquatic life stages, such as mosquitoes (Diptera: Culicidae), by creating and/or sustaining ephemeral ponds used for egg and larval development (Corbet and Danks 2012). Such biological differences among arthropod groups suggest that responses to shrub expansion are likely to be taxon-specific. However, our current knowledge is limited because most previous analyses on shrub-associated arthropod

communities have been conducted at the level of arthropod orders, which group lower taxa from a variety of ecological niches that may have disparate responses to shrub dominance (but see Legault and Weis 2013, Hansen et al. 2016).

To address the need for greater specificity in our understanding of arthropod responses to vegetation change in the Arctic, I collected arthropods via pitfall trapping and sweep-netting across a tundra-shrub ecotone in northwestern Alaska for two summers (Chapter 2). I analyzed 20 taxonomic groups of arthropods by guild (herbivore, predator, pollinator, parasitoid) to discern how abundance of species with different ecological functions was affected by habitat characteristics, including vegetation cover, height, and landscape characteristics. To predict community-level responses to changes in vegetation, I then analyzed total arthropod abundance, total biomass, diversity, and community composition in response to shrub cover, shrub height, and landscape characteristics.

Changes in arthropod abundance and biomass associated with increased shrub cover may directly influence higher trophic levels, particularly predaceous arthropods and vertebrate insectivores. Primary predators of arthropods in the Arctic are migratory songbirds and shorebirds, which rely on arthropods as an essential source of protein. Arthropods are particularly important in nestling diet, and many omnivorous species of birds are strictly insectivorous during the nestling period (Maher 1979, Boelman et al. 2015). To understand potential impacts on birds of changes in prey abundance, we must understand their dietary preferences and how use of invertebrate prey corresponds to its local availability. To address these questions I used next-generation sequencing of nestling fecal matter to characterize the nestling diet of 5 common insectivorous migratory passerines (Chapter 3).

Next-generation sequencing (NGS) is a relatively new sequencing technology that uses short (<500 base-pair) fragments to sequence DNA from many animals simultaneously. It has been used widely in diet studies of mammals (Bohmann et al. 2011, Bowles et al. 2011, Razgour et al. 2011, Zeale et al. 2011, Hamad et al. 2014), and applications to avian diet have recently been developed (Jedlicka et al. 2013, Crisol-Martinez et al. 2016, Jedlicka et al. 2017). Previous genetic studies of avian fecal matter have revealed important ecological relationships between birds, arthropod prey, and plants, such as control of herbivorous insects in vineyards and macadamia plantations (Crisol-Martinez et al. 2016, Jedlicka et al. 2017). Understanding such top-down interactions is important in the context of rapid vegetation change in the Arctic.

To understand the role of insectivorous passerines in Arctic food webs and predict the birds' vulnerability to changes in arthropod availability, I analyzed the significance of spatial, temporal, and ecological influences on nestling diet composition. Arthropods were collected concurrently with fecal samples to test if availability was a significant predictor of prey use. By comparing arthropod communities that currently exist across a gradient of tundra- and shrub-dominated vegetation, we can gain a better understanding of how future vegetation change may affect the arthropod and songbird communities in Arctic areas. In this thesis I present a detailed analysis of how the arthropod community is related to shrub cover and describe potential effects on migratory songbirds from continued shrub expansion in the Arctic.

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CHAPTER 2. ARTHROPOD COMMUNITIES ACROSS TUNDRA-SHRUB ECOTONES OF NORTHWESTERN ALASKA: IMPLICATIONS OF CONTINUED SHRUB EXPANSION[1]

2.1 ABSTRACT

Arthropods play an important role in the structure and functioning of Arctic ecosystems. Not only do they serve as complex linkages between plants and higher-level predators in food webs, they also provide key ecosystem services such as pollination and nutrient cycling. Changes in vegetation structure can alter the physical habitat structure, thermal environment, and food available to arthropods, thereby having the potential to induce cascading effects throughout the ecosystem. Across the Arctic, taller woody shrubs, particularly willow (*Salix* spp.), birch (*Betula* spp.), and alder (*Alnus* spp.), have been expanding rapidly onto tundra. In this study we examined the relationships between the abundance, diversity, and community composition of arthropods and the height and cover of several shrub species across a tundra–shrub ecotone in northwestern Alaska. We found that abundance and biomass of arthropods were most strongly and consistently associated with the amount of willow cover, which also was associated with significant shifts in arthropod community composition and diversity. For each shrub type, cover usually had greater explanatory power than height, suggesting that plant composition, not physical structure, is a more important influence on arthropod communities. Taken together, our results suggest that shrub expansion could result in a significant shift in Arctic food-web structure and an increase in food availability for insectivores, although future ecosystem change

[1] McDermott, M. T., P. Doak, C. M. Handel, G. A. Breed, and C. P. Mulder. Arthropod communities across tundra-shrub ecotones of northwestern Alaska: Implications of continued shrub expansion. In preparation for submission to Oikos.

in the Arctic is likely to be heterogeneous as these shrub types are expanding at different rates and in different places across the Arctic.

2.2 INTRODUCTION

Vegetation structure in the Arctic is changing due to warmer temperatures, longer summers, and thawing permafrost (Sturm et al. 2001, Tape et al. 2006, Lantz et al. 2012). The expansion of woody shrubs, particularly willow (*Salix* spp.), birch (*Betula* spp.) and alder (*Alnus* spp.) around waterways, is occurring across the Arctic (Tape et al. 2006), and there is substantial experimental evidence that increased air temperature drives increases in shrub cover and height in low Arctic areas (Elmendorf et al. 2012). Increased fire frequency, expected with continued climate change, may accelerate the establishment of deciduous shrubs, particularly willow, on tundra (Racine et al. 2004).

An increase in shrub cover has the potential to impact Arctic animal community structure and ecosystem function (Post et al. 2009, Thompson et al. 2016). Increases in shrub cover, height, and density decrease plant diversity and alter the structure and composition of tundra habitats (Myers-Smith et al. 2011). Shrub thickets change solar radiation, soil moisture, soil temperature, and snow cover by providing shade in summer and accumulating snow in winter (Myers-Smith et al. 2011, Lantz et al. 2012, Sweet et al. 2014).

Understanding the impact of shrub expansion on arthropods is particularly important due to their abundance, diversity, and role in ecological processes in the Arctic (Meltofte et al. 2013). Arthropods are a large component of terrestrial Arctic biodiversity, with an estimated 1,650 to 3,500 species of insects alone (e.g. Danks 1992, Foottit and Adler 2009, Hodkinson et al. 2013) compared to 873 species of vertebrates and 2,220 species of plants (Meltofte et al. 2013). In

addition, arthropods provide a wide variety of ecosystem services in the Arctic, including pollination, nutrient cycling in soils, decomposition of organic matter, predation, parasitism, and food for predaceous arthropods and vertebrates (e.g. Danks 1992, Foottit and Adler 2009, Hodkinson et al. 2013). Many migratory birds depend on arthropods for protein, and songbird and shorebird nestlings often feed exclusively on arthropods (e.g. Danks 1992, Boelman et al. 2015, Pérez et al. 2016).

An essential step in predicting the cascading ecological effects of shrub expansion is understanding the mechanisms by which vegetation affects the abundance, community composition, and biodiversity of arthropods. As small ectotherms in a cold environment, Arctic arthropods are strongly influenced by temperature and fine-scale habitat structure. Previous research suggests that at a local scale, plant species composition is a better predictor of arthropod community structure (species composition and relative abundance) than abiotic variables (Schaffers et al. 2008, Bowden and Buddle 2010) and therefore vegetation change may result in changes in the abundance and distribution of arthropods in the Arctic. Research in Arctic Alaska has found that overall arthropod abundance, and fly (Diptera) abundance in particular, increases with shrub dominance (Rich et al. 2013), and that arthropod biomass is positively related to the normalized vegetation difference index (NDVI) or 'greenness' (Sweet et al. 2015). Since NDVI increases with shrub cover and height (Boelman et al. 2011, Sweet et al. 2015), these results suggest that arthropod biomass is correlated with shrub dominance.

Most studies of the ecological impacts of shrub expansion have grouped plants by growth form (i.e. deciduous shrubs, graminoids, forbs, etc.) (Rich et al. 2013, Boelman et al. 2015). Although this is a useful way to assess the response of arthropods to general types of Arctic vegetation, it fails to address important biological differences among shrub species. Given

differences among shrub taxa in the rate and spatial extent of expansion (Elmendorf et al. 2012, Myers-Smith et al. 2011) and the resources they provide to arthropod herbivores, pollinators and associated natural enemies (MacLean and Jensen 1985, Mulder 1999, Strong et al. 1984), the taxonomic identity of shrubs will influence arthropod response and the resulting ecological effects of shrub expansion. Thus, our ability to predict ecological outcomes of shrub expansion would be improved by a more detailed examination of the responses of Arctic arthropods to specific plant taxa.

Despite the Arctic Council's call for a better understanding of how arthropod biology and biodiversity might respond to climate change (Hodkinson et al. 2013), the relationship between Arctic arthropod biodiversity and vegetation change is just beginning to be explored (Rich et al. 2013, Ernst et al. 2016, Hansen et al. 2016). Shrub expansion increases the structural complexity of vegetation but decreases plant diversity (Post et al. 2009), leading to potentially counteracting forces on arthropod diversity. Increased vertical structure creates more spatial niches and has been shown in many systems to support a greater diversity and abundance of arthropods (Strong et al. 1984). Although some studies have documented a positive relationship between plant diversity and arthropod diversity (Siemann et al. 1998, Haddad et al. 2001), there is evidence that the response of arthropods to plant diversity varies among arthropod taxa (Jeanneret et al. 2003), and many studies also provide evidence that plant species composition and structural characteristics exert a stronger influence than plant diversity on arthropod diversity as a whole (Halaj et al. 2000, Koricheva et al. 2000). Prior research has found increased richness and biodiversity in shrub thickets for some taxa (Rich et al. 2013), although it is unclear if this pattern holds for all arthropods. Given these contrary relationships, without empirical evidence

we cannot predict how arthropod richness, evenness, and diversity are likely to shift with shrub expansion.

Research and analysis on Arctic arthropod biodiversity and ecology have been limited by the difficulty of arthropod identification below the order level for non-entomologists and the tendency for entomologists to specialize on one or a few taxonomic groups, with spiders and butterflies best represented in the literature. Lower-level identifications are particularly important where there is variety in ecological function, and many arthropod orders (e.g. Coleoptera, Diptera) contain species from multiple guilds (herbivore, predator, parasitoid, decomposer, scavenger) (Triplehorn and Johnson 2005). However, exhaustively cataloging all arthropod species in a study area is time-consuming and requires expertise outside the scope of most ecological research programs. To balance these concerns, in the current study we endeavored to identify all arthropods to family level, enabling us to classify most specimens according to ecological function since many families were composed of only one trophic group.

Because arthropods occupy many trophic levels and provide a wide variety of ecosystem services, investigations of family-level responses to shrub expansion should improve our understanding of the downstream effects of changes in arthropod communities. By studying existing tundra–shrub ecotones, we can use a space-for-time approach to provide evidence for how continued shrub expansion may affect arthropod communities, and thus greater clarity about how the Arctic may continue to change with increased warming.

Toward this goal, we tested four hypotheses:

1. The responses of overall arthropod abundance, biomass, and diversity will differ among shrub taxa.
2. Abundance of each arthropod taxon will be significantly related to shrub cover, but the

direction and magnitude of this effect will depend on the functional and ecological traits of each arthropod group. We expect herbivores to have the strongest and most positive associations with palatable shrub taxa due to increased plant biomass, and we expect most pollinators to be positively associated with ericaceous shrubs that provide nectar and pollen. The responses of predators are likely mediated by changes in prey availability and are difficult to predict based on our lack of knowledge on specific predator-prey associations in our study system.

3. Overall arthropod abundance and biomass will increase with shrub height due to greater vertical habitat area.
4. Arthropod taxonomic richness will be greater in tall shrubs due to a wider variety of niches, but evenness may not show the same trend due decreased plant species diversity and the resulting numerical dominance of a few herbivorous insects (e.g. aphids, psyllids) in shrub habitats (MacLean 1983, MacLean and Jensen 1985).

2.3 METHODS

2.3.1 Study System

Our research took place on Alaska's Seward Peninsula (Figure 2.1), which is known as a biodiversity hotspot in the Holarctic (Hope et al. 2015) and is part of Beringia, an internationally recognized area of conservation importance (Hodkinson et al. 2013). This 52,000 km^2 area experiences highly variable weather with conditions that range from snowstorms in July to dry periods with temperatures above 32°C and encompasses 21 major habitat types (Kessel 1989). Situated in the transition zone between boreal forest and tundra, the Peninsula is currently undergoing rapid climatic and vegetation changes including shrub expansion into former tundra

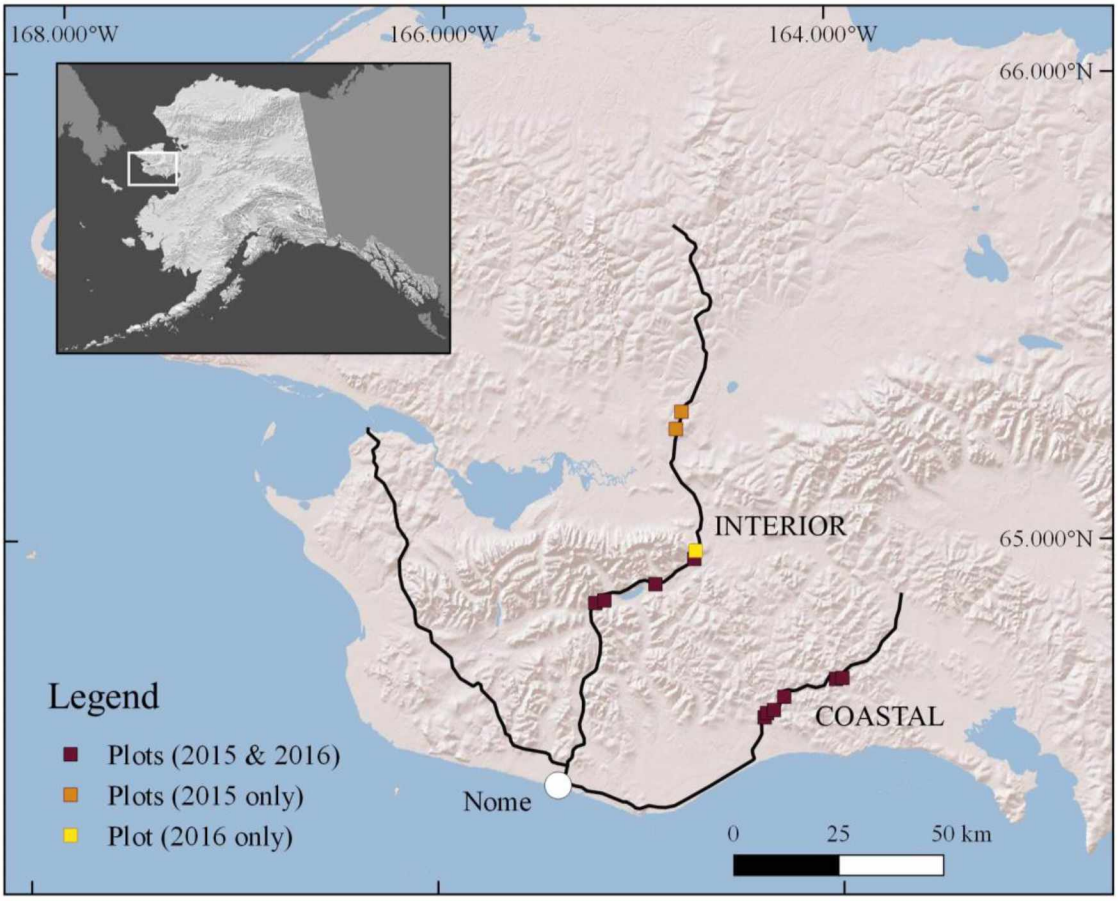

Figure 2.1 Location of 13 plots at our coastal and interior sites on the Seward Peninsula, northwestern Alaska, USA, and the years in which arthropods were sampled. Inset shows study region location within Alaska. In all cases except one 2016 plot (indicated in yellow), each pair of adjacent plots included one tundra-dominated plot and one shrub-dominated plot within 4 km of each other.

vegetation (Racine et al. 2004, McNew et al. 2013). From 1986 to 1999, shrubs advanced about 100 m northwest and 14% of the Peninsula increased in canopy cover, compared to 5% that decreased in canopy cover and 80% that remained stable (Silapaswan et al. 2001). These vegetation changes are most pronounced around drainage-ways, where moist soil and a deep active layer provide ideal conditions for accelerated shrub growth (Sturm et al. 2001, Tape et al. 2006).

This research was conducted during the summers of 2015 and 2016 as part of the US Geological Survey's (USGS) Changing Arctic Ecosystems initiative, which has a broad goal of

understanding how climatic factors influence avian distribution, abundance and demographics across the boreal–Arctic transition zone (McNew et al. 2013). Thus, sampling for the arthropod research reported here was designed in conjunction with migratory bird monitoring.

To investigate the relationships among climatic factors, vegetation, arthropods, and migratory birds over a large geographic area and under a variety of conditions, we established 600-m × 600-m plots at two study sites, one interior and one coastal (Figure 2.1). In 2015, we initially established 12 plots as pairs that contrasted in dominance of tundra vegetation vs. taller shrubs, with three pairs of plots at each study site. Tundra areas on our plots were characterized by graminoid vegetation (primarily *Carex* spp., *Poa* spp., *Eriophorum* spp., and *Festuca* spp.), low (<0.4 m tall) ericaceous shrubs (primarily *Vaccinium uliginosum, V. vitis-idea,* and *Empetrum nigrum*), and prostrate willow (*S. arctica, S. polaris, S. pulchra)* (Figure 2.2a). Taller shrub areas were characterized by stands of willow *(Salix pulchra, S. planifolia, S. richardsonii,* and *S. alaxensis*), birch *(Betula nana* and *B. glandulosa)*, and/or mountain alder *(Alnus viridis* ssp. *crispa)* >0.4 m tall (Figure 2.2b). Most of the study plots were quite heterogeneous in terms of vegetation,

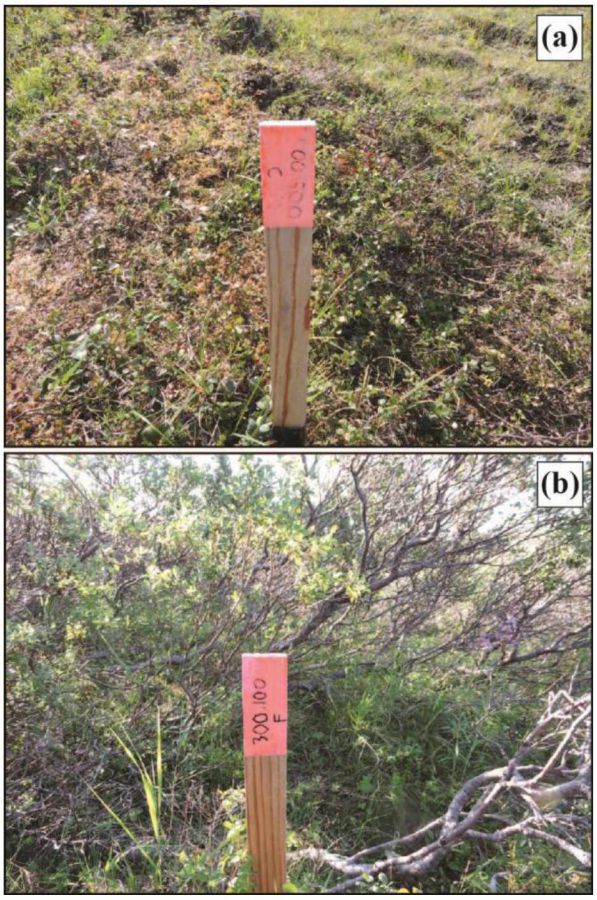

Figure 2.2 Photos taken near pitfall arrays in northwestern Alaska, USA, showing **(a)** typical tundra vegetation characterized by graminoids and mixed low ericaceous shrubs and **(b)** mixed willow and birch shrub thicket. Wooden stakes extend about 0.6 m above soil surface.

with shrub and tundra interspersed; therefore all of our analyses consider vegetation characteristics at finer spatial scales (see below). In 2016, we replaced one pair of plots on the interior study site with a new single tundra-dominated plot due to the inaccessibility and low numbers of breeding birds on the original plot pair. We therefore have 2 years of data for 10 plots and 1 year of data for 3 plots (Figure 2.1).

2.3.2 Arthropod Sampling

We used two techniques to sample the abundance and diversity of arthropods over the gradient of habitats available on each plot. Sweep-netting targeted flying and canopy-dwelling arthropods such as flies (Diptera) and caterpillars (Lepidoptera), and pitfall trapping targeted ground-dwelling arthropods such as some families of beetles (Coleoptera) and spiders (Araneae) (Sorenson et al. 2002, Doxon et al. 2011). Taken together, these sampling methods provided a relatively complete picture of the above-ground arthropod community in each study area. Although pitfalls captured some soil-dwelling invertebrates, abundance estimates were not reliable for these groups, and these species were excluded from analysis. To sample when arthropods were most active and available as a food source for migratory birds, we collected arthropods weekly during the warmest period of the year and the peak breeding season for migratory birds (8 June–28 July in 2015; 3 June–27 July in 2016).

We established three pitfall arrays 200 m apart in a line through the center of each plot. Arrays consisted of three cups (7.6 cm diameter; 16.5 cm tall) buried flush with the soil surface and placed in a triangle 1 m apart. Each cup contained 2 cm of propylene glycol and was covered with a plywood square propped 3–4 cm above the rim of the cup so that the cup was not flooded by rainwater and arthropods could move unimpeded to the rim. All three cups in an array were

emptied weekly and combined into a single sample for identification and analysis. There were seven weekly collection periods each season.

Sweep-net transects consisted of 50 side-to-side sweeps usually beginning at one of the pitfall arrays (see below for exceptions) and extending 25 m in a random direction on each sampling date. The net was aimed to sweep the top 25% of vegetation within a 2-m swath along the transect line. We conducted two (in 2015) or three (in 2016) sweep-net transects per plot each week for a total of eight weekly sweep-net sampling periods each year. One sample period is missing from one point due to wet weather, and this point was excluded from analysis.

Arthropod samples were sorted and identified to family for most groups using published keys (Triplehorn and Johnson 2005, Marshall 2006), although some (Lepidoptera, Araneae, Schizophora) were sorted to higher taxonomic levels due to the difficulty in distinguishing families of these groups and a lack of published keys for Arctic taxa. See Table 2-A.1 in Appendix 2-A for identifications used and counts of individuals.

We dried 30 individuals of each family of arthropods for 48 hours at 40°C and used mean individual dry mass to calculate biomass from counts of individuals. For rare taxa with fewer than 30 specimens we measured as many individuals as possible. When size was highly variable within a taxon, we separated individuals by length and measured the biomass of each size class. We then multiplied counts of arthropods from all samples by mean mass of each taxon and size class. See Table 2-A.2 in Appendix 2-A for biomass data.

Individuals within each taxon were counted and weighed separately by life stage (larva, nymph, adult), but life stages were combined for analyses of biodiversity and abundance. Sweep-net samples and pitfall samples were analyzed separately.

2.3.3 Habitat Sampling

To gather information about relevant habitat features, we characterized vegetation within a series of 0.5-m × 0.5-m quadrats during the year in which each plot was established. Vegetation sampling took place over a 3-week period in mid to late July, after most tundra plants had reached peak greenness and change in biomass was relatively slow (Sweet et al. 2015). Five quadrats were placed at 5-m intervals along one 20-m randomly oriented transect associated with each arthropod sample point. Within each quadrat, we estimated percent cover for the following 11 categories: tall willow (*Salix alaxensis, S. glauca, S. pulchra, S. richardsonii*), dwarf willow (e.g., *S. arctica, S. phlebophylla, S. polaris, S. reticulata*), birch (*Betula nana* and *B. glandulosa*), alder (*Alnus crispa*), ericaceous shrubs (primarily *Vaccinium uliginosum, V. vitis-idea, Empetrum nigrum, Cassiope tetragona, Ledum decumbens,* and *Arctostaphylos alpina*), graminoids (primarily *Carex bigelowii, C. aquatilis, Poa arctica, Festuca altaica, F. rubra, Eriophorum vaginatum, E. angustifolium,* and *Calamagrostis canadensis*), forbs, lichens, mosses, bare ground, and water. Although willow species that form tall shrub patches may also grow as prostrate shrubs in tundra, we classified all willows into two categories (tall and dwarf) characterized by species rather than by height. This allowed us to distinguish between the willow species that have the potential to grow tall and the dwarf willow species that seldom exceed 30 cm in height. Similarly, we grouped ericaceous shrubs since all are slow-growing and short (usually < 30 cm). In each quadrat we also measured maximum and modal height of graminoids and each shrub type, permafrost depth, soil temperature 20 cm below soil surface, and vegetation density. Modal height of vegetation was recorded as the most common of several height measurements within a quadrat rounded to the nearest centimeter. Vegetation density was measured by placing a pole perpendicular to the soil surface in the center of each quadrat and

recording the lowest point visible from 2 m north at 0.5 m above the soil surface; lower values indicated less dense vegetation. Elevation was measured using a handheld GPS unit (64s or 74, Garmin International, USA) with error ± 3m. Slope was measured with a clinometer over 10 m, and aspect was determined as the direction over 10 m with maximum downslope.

2.3.4 Statistical Analysis

All statistical analyses were conducted using R version 3.2.2. (R Core Team 2015). We built linear mixed-effects models (LMEMs) using the R package 'lme4' and generalized linear mixed models (GLMMs) with the R package 'glmmADMB' (Fournier et al. 2012, Bates et al. 2015). We estimated diversity metrics and examined community composition using non-metric multidimensional scaling (NMDS) with the R package 'vegan' (Oksanen et al. 2015).

2.3.4.1 Data preparation.

To retain sample size while reducing points with high leverage, outliers in predictors and covariates were truncated to the next highest value (Osborne and Overbay 2004). Changes to each covariate and response variable are listed in Table 2-C.1 in Appendix 2-C. Counts of arthropods were aggregated across the season for each collection point, so each data point represents the sum of 7 (pitfall) or 8 (sweep) samples taken periodically at one location. In a few cases when pitfalls had been open for 6 or 8 days instead of 7, the counts of insects caught were adjusted by multiplying counts by a correction factor so that all pitfall abundance estimates were normalized to an equivalent of 168 trap-hr (7 days). To address potential multicollinearity, Pearson correlation coefficients were calculated for the suite of candidate predictors in a model and all predictors had coefficients <0.4, with the exception of linear and quadratic terms for the same variable.

2.3.4.2 Overall abundance and biomass.

The goal of this analysis was to determine the influence of shrub characteristics on overall arthropod abundance and biomass while ensuring a reasonable model fit by including important abiotic variables. To meet this goal, we included cover or height of tall willow, birch, and ericaceous shrubs, as well as slope and aspect. Since aspect is a circular variable measured in degrees, we converted it into two linear variables to use as predictors, 'northness' and 'eastness', by taking the cosine and sine, respectively. Initially we also considered the influence of dwarf willow, graminoids, lichens, mosses, vegetation density, and elevation, but these variables were rarely significant and tended to have small effect sizes in explaining overall and taxon-specific abundance. To reduce our candidate set of predictor variables we excluded these vegetation variables from our final analysis and focused on tall willow (hereafter referred to as 'willow'), birch, and ericaceous shrubs. Although willow, birch, and alder are responsible for most of the recent increases in shrub vegetation in Arctic Alaska, ericaceous shrubs have been shown to increase modestly in cover and height in some tundra areas after experimental warming (Elmendorf et al. 2012). Alder is a fairly common shrub species that has increased in cover on the Seward Peninsula in recent decades (Tape et al. 2006), but it was observed on only one of our vegetation transects and was not included in our analyses.

In our abundance models, the response variable was the number of individual arthropods; therefore we limited possible distributions to Poisson and negative binomial. We first tested the data for overdispersion as outlined by Cameron and Trivedi (1990) with the R package 'AER' (Kleiber and Zeileis 2008) and then compared the fit of a negative binomial model and Poisson model using Akaike's Information Criterion (AIC) (Burnham and Anderson 2003). If diagnostics indicated potential zero-inflation, we calculated AIC scores for fit of the data to Poisson,

negative binomial, zero-inflated Poisson, and zero-inflated negative binomial distributions and selected the distribution with the lowest AIC value. We inspected the residuals and the predicted vs. observed values to assess model assumptions and model fit. In all cases, a non-zero-inflated negative binomial distribution provided the best fit to the abundance data.

We tested total biomass data for normality with the Shapiro-Wilk test since they did not meet the assumptions of other known distributions. We excluded one pitfall point with high leverage (leverage >0.8) and identified an appropriate transformation to normalize the data with the Box-Cox procedure. We then analyzed the transformed data with linear mixed-effects models.

Our sets of candidate models considered random effects for year, site, and plot to account for variation that was not directly relevant to our research questions. Exploratory analyses revealed little interannual variation in overall abundance and abundance of most individual taxa. Random-effects structures were compared with AIC scores, and if year did not improve model fit it was dropped to aid in convergence. Site and plot were retained as random effects in all models since they were integral parts of the research design (Barr et al. 2013).

Habitats with a mixture of shrub vegetation and open tundra may be more suitable for arthropods due to increased solar radiation and plant diversity (Horvath et al. 2000, Pinheiro et al. 2010). To allow for potential non-linear relationships of arthropods with shrub cover, we included both linear and quadratic terms for each shrub variable. The full models for total abundance and biomass of arthropods included slope, aspect, shrub variables (cover or height), and random effects. We selected either cover or height of willow, birch, and ericaceous shrubs by comparing AIC scores of the full model with other shrub variables included as percent cover. Non-significant terms were eliminated sequentially and AIC was used to choose the final model.

2.3.4.3 Taxon-specific abundance.

We selected the five most abundant orders (Araneae, Coleoptera, Diptera, Hemiptera, and Hymenoptera, together representing 97% of total abundance) to examine taxon-specific relationships between arthropod abundance and vegetation characteristics. To examine potential heterogeneity among lower taxonomic levels within these orders, we selected all groups that made up at least 1% of overall abundance for additional analysis (Coleoptera: Carabidae and Staphylinidae; Diptera: Chironomidae, Culicidae, Empididae, Phoridae, Sciaridae, and Schizophora; Hemiptera: Aphididae, Cicadellidae, Delphacidae, Miridae, and Psyllidae; Hymenoptera: Tenthredinidae, Braconidae, Chalcidoidea, and Ichneumonidae; Lepidoptera: larvae). If a clear majority of individuals (>60%) from a group were collected in one sample type (pitfall trap or sweep-net), then our analysis considered counts from only that sample type (e.g., 87% of Cicadellidae were caught in sweep-nets so we used sweep-net counts only). Only 2 taxonomic groups (Hymenoptera: Chalcidoidea and Diptera: Schizophora) were abundant in both pitfall traps and sweep-nets, and for these we performed a separate analysis for each sample type.

Initial analyses indicated that across shrub taxa, cover was more often significant and tended to have larger effect sizes than height. Therefore in our analysis of taxon-specific abundance of arthropods, we limited fixed effects to slope, aspect, and shrub cover variables to allow more direct comparisons among candidate models. Model selection then proceeded as outlined for overall abundance (see above). We plotted the relationship of taxon-specific abundance to shrub cover from the top model by generating predicted values for each shrub variable while holding all other variables at their mean values. Coefficients for each final model are detailed in Table 2-C.2 in Appendix 2-C.

2.3.4.4 Diversity.

We calculated taxonomic richness, evenness, and the Shannon-Weaver diversity index (H) for arthropods at each collection point for which samples were sorted and identified in both 2015 and 2016 (n = 54 for pitfall, n = 50 for sweep-net). Sampling effort was equal across all points within a given sampling technique, allowing us to compare diversity estimates directly (Scheiner et al. 2000, Gotelli and Colwell 2001). Each taxon was consistently identified to the same taxonomic level (order, family, or superfamily) across samples, so these diversity indices provide a useful comparison between habitat types within the framework of the current study.

We analyzed separate linear mixed models for the three response variables (richness, evenness, and diversity), and considered each response independently for sweep-net and pitfall samples. For all models data were tested for normality and heterogeneity of variance. Data for richness of pitfall samples were square-root transformed to improve normality of the residuals. To determine the relative influence of shrub structural characteristics on diversity, we first selected cover or height for each tall shrub taxa based on AIC scores while including slope, aspect, and all other shrub types as percent cover (Table 2-C.3 in Appendix 2-C). We then performed the same model-selection procedure described above.

2.3.4.5 Community composition.

To examine how vegetation characteristics influenced the arthropod community as a whole, we used NMDS, an ordination technique that analyzes and visualizes community similarity. We used the Bray-Curtis index of dissimilarity to calculate a single metric for each pair of sampling points based on counts of arthropod taxa, in this case, families or orders. We then used this matrix to create a two-dimensional plot that visualizes community dissimilarity. To assess the influence of vegetation variables on community composition, we conducted a

permutation test between the dissimilarity matrix and shrub characteristics. We randomly arranged the order of shrub variable observations, effectively assigning them to a different sample point, and calculated the correlation coefficient (r) between arthropod community dissimilarity and the rearranged vegetation community dissimilarity to generate a null distribution (number iterations = 999). We assessed the significance of each shrub characteristic by comparing the correlation coefficient of the original data to this null distribution.

2.4 RESULTS

We identified 39,502 individual arthropods from 20 orders (Table 2-A.1 in Appendix 2-A) in 483 pitfall samples and 504 sweep-net samples. Herbivores were most common (46% of individual arthropods) followed by predators (24%; Table 2.1). The most abundant orders were Hemiptera (42.1%), Diptera (21.7%), Araneae (13.1%), Hymenoptera (10.9%), and Coleoptera (9.3%). In pitfall traps, the most abundant taxa were predaceous: Araneae (34.2% of individuals) and Coleoptera: Carabidae (15.9%). In sweep-net samples, the most abundant taxa were herbivorous: Hemiptera: Psyllidae (34.2%) and Hemiptera: Cicadellidae (16.6%).

Tall willow species were present on vegetation transects within most study plots and were typically

Table 2.1 Relative abundance (%) by ecological guild of total arthropods (n = 39,502) collected during summer in 2015 and 2016 in pitfall and sweep-net samples in northwestern Alaska, USA.

Guild	%
Primary	
Herbivore	45.89
Predator	24.08
Other	20.67
Parasitoid	9.01
Fungivore, detritivore, scavenger	0.35
Secondary*	
Pollinator	9.12
Parasite (Blood-sucking insect)	2.60

*Secondary guilds always overlapped with a primary guild (e.g., a pollinator was also a predator) so percentages sum to >100%.

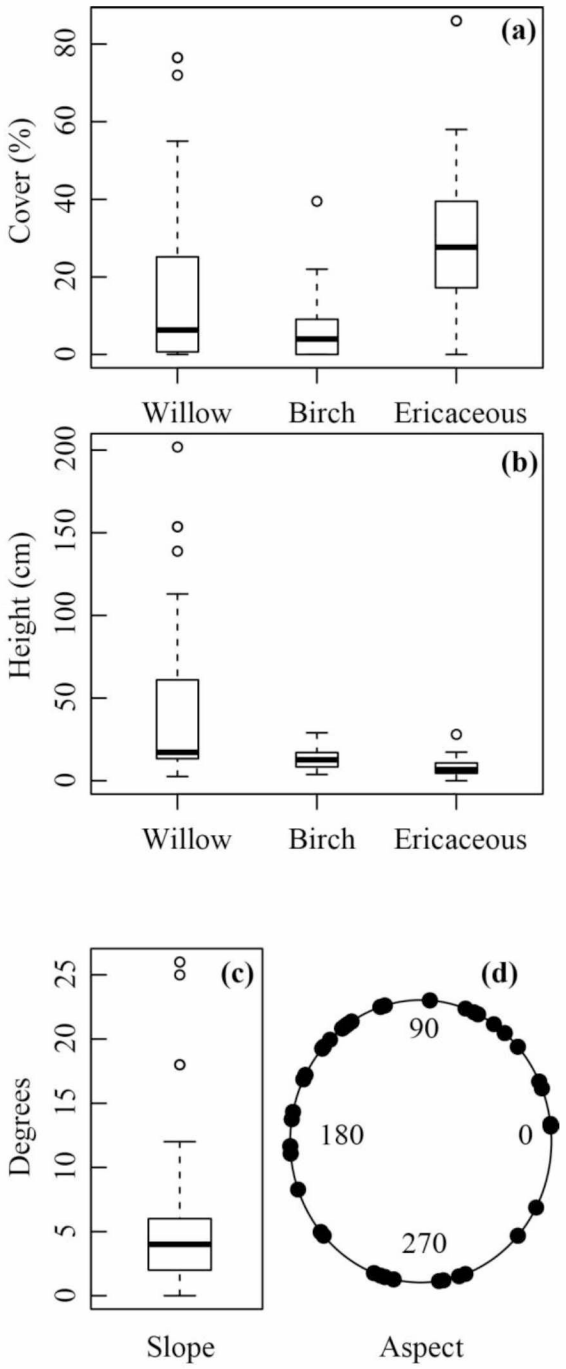

Figure 2.3 Vegetation **(a,b)** and landscape **(c,d)** variables measured over 69 transects on the Seward Peninsula, USA, and used as predictors of arthropod abundance, biomass, and diversity. Boxplots **(a,b,c)** show the median (bold line) and 1st and 3rd quantiles of the data distribution (upper and lower box edges, respectively).

less than 50 cm tall, but a few transects included very tall thickets (Figure 2.3a,b). Ericaceous plants were present on almost every transect, but tended to be short. Birch was present on just over half of the transects and was usually less than 20 cm, although we had a few observations of birch shrubs almost a meter tall. Cover and height measurements given here are before truncating variables with skewed distributions and may differ slightly from the data shown in Figure 2.3. Descriptions of additional vegetation and landscape variables are shown in Figures 2-B.1 and 2-B.2 in Appendix 2-B. Details on truncation of the maximum value of predictors are given in Table 2-C.1 in Appendix 2-C.

2.4.1 Overall Abundance

Arthropod abundance was more strongly related to willow and ericaceous cover than height. For pitfall samples overall abundance was positively related to willow cover (Table 2.2, Figure 2.4a) and had a positive-curvilinear relationship to willow cover in sweep-net

samples, with the highest predicted abundance at 75% cover, close to the maximum willow cover we sampled (Figure 2.4a). Ericaceous cover was a negative predictor of pitfall abundance, but a slightly positive and curvilinear predictor of sweep-net abundance (Table 2.2, Figure 2.4c,d). Neither birch height nor cover were in the final model of abundance for either sample type (Figure 2.4e,f). See Table 2-C.4 in Appendix 2-C for candidate models and associated AIC scores. Slope had a negative relationship with the abundance of arthropods in pitfall traps, but was not included in the final model of arthropod abundance in sweep-net samples (Table 2.2). Aspect was not significant in explaining overall abundance from either sample type.

Table 2.2 Final models for total abundance and biomass of arthropods collected in pitfall and sweep-net samples during summer in 2015 and 2016 in northwestern Alaska, USA. Estimated parameters and significance are shown for each fixed effect included in best models from AIC model selection procedure. Models for each response variable included the random effects in parentheses: abundance in pitfalls (year, site, plot); abundance in sweep-nets (site, plot); biomass in pitfalls (site, plot); and biomass in sweep-nets (site, plot).

Response	Sample Type	Parameter	Estimate	*P*
Abundance	Pitfall	Willow Cover	0.007	<0.001
		Ericaceous Cover	-0.005	0.019
		Slope	-0.029	<0.001
	Sweep-net	Willow Cover	0.036	<0.001
		Willow Cover^2	-0.0002	0.073
		Ericaceous Cover	-0.007	0.440
		Ericaceous Cover^2	0.0002	0.123
Biomass	Pitfall	E aspect	-2.192	0.102
		Slope	-0.601	0.019
	Sweep-net	Willow Cover	0.117	<0.001
		Birch Height	0.120	0.003

2.4.2 Overall Biomass

Total arthropod biomass data were not normally distributed for either set of samples (Shapiro-Wilk test: pitfall, $P < 0.001$; sweep-net, $P = 0.003$) but using the square-root transformation improved normality (Shapiro-Wilk test: pitfall, $P = 0.187$; sweep-net, $P = 0.348$)

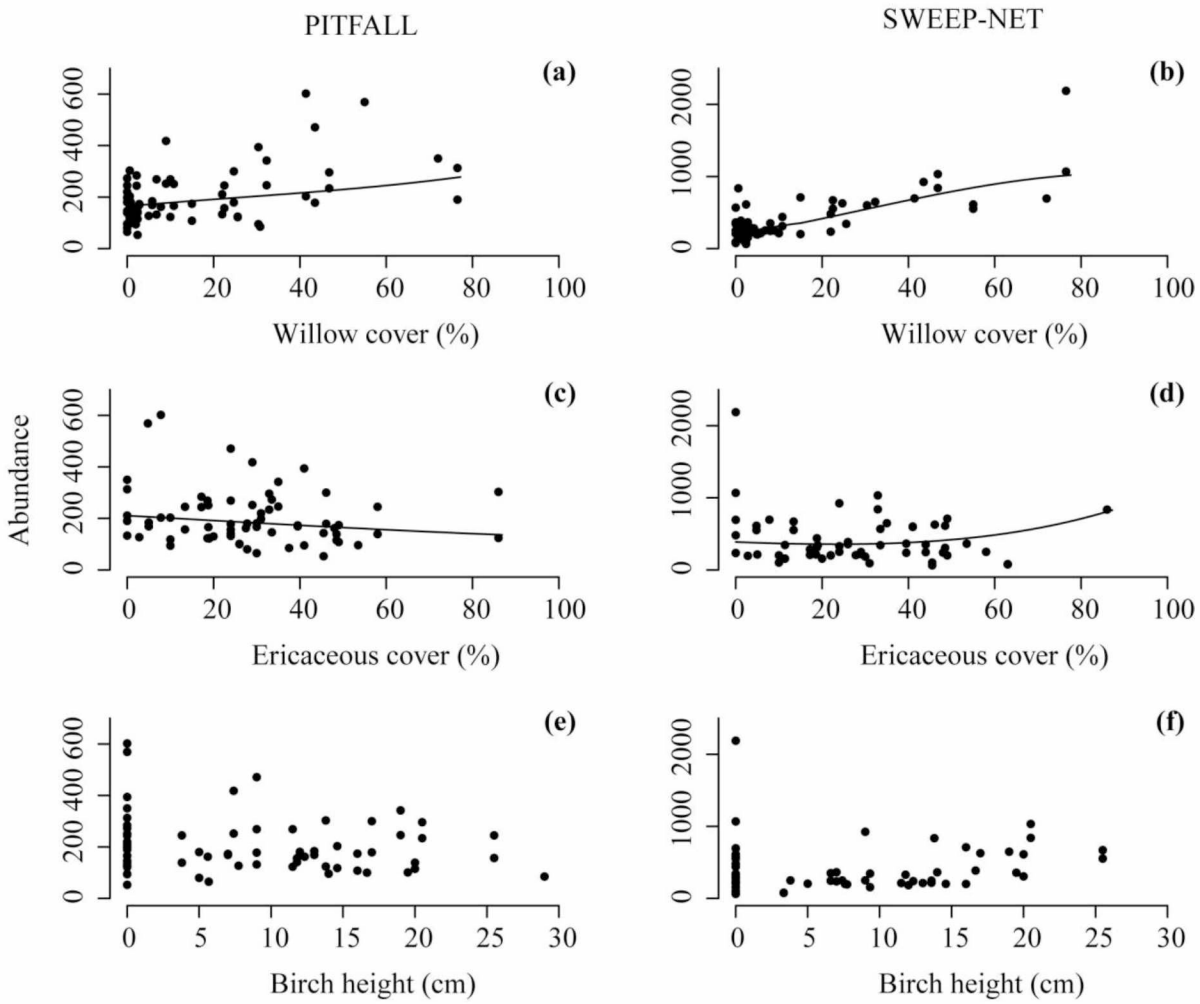

Figure 2.4 The relationship of willow cover, ericaceous cover, and birch height to total abundance of arthropods caught in pitfall traps (a,c,e) and sweep-nets (b,d,f) in northwestern Alaska, USA. All variables were in final model except birch height (e,f). Lines show predicted relationship of abundance to each vegetation characteristic from the best-fitting models described in Table 2.2.

and homogeneity of variance in the residuals. Biomass of arthropods in pitfall samples was influenced primarily by abiotic variables and had a negative relationship with east aspect and slope, but no significant relationship with shrub characteristics (Table 2.2). In sweep-net samples, willow cover was a better predictor of biomass than willow height and was positively related to biomass (Table 2.2). Birch height was a better predictor of biomass than birch cover and was also positively related to biomass (Table 2.2). Total biomass in sweep-net samples was not significantly related to ericaceous cover, ericaceous height, slope, or aspect. See Table 2-C.5

in Appendix 2-C for candidate models and associated AIC scores. Plot and site, but not year, contributed to variation in biomass in both sample types and were included as random effects.

2.4.3 Taxon-specific Abundance

For most taxonomic groups of arthropods, abundance was more strongly related to vegetation variables, particularly willow cover, than to abiotic factors. Willow cover was almost always in the final model of abundance (19/20 families*life stages, 4/4 orders), and this relationship was usually positive (7/20 families*life stages, 2/4 orders) or curvilinear with abundance peaking at about 50% cover (9/20 families*life stages, 2/4 orders) (Figure 2.5). In contrast, ericaceous cover and birch cover were not in the final model of abundance for many groups. When abundance was related to ericaceous or birch cover, the shape (linear vs. quadratic) and sign (positive vs. negative) of these relationships varied across taxa.

There was heterogeneity in response to each type of shrub within each arthropod order. For example, most Hemiptera were positively associated with willow cover, except two families (Cicadellidae and Delphacidae) known to use graminoids as host plants (Richardson et al. 2002, Hamilton and Whitcomb 2010) (Figure 2.5). The response of dipterans to ericaceous shrubs was usually positive, however, ericaceous cover was not included in the final model of abundance for Culicidae, Sciaridae, and Schizophora (from pitfalls) (Figure 2.5).

Only seven taxonomic groups had a significant relationship with birch cover and these came from varying orders. The response of arthropod taxa to birch cover was variable, but several taxa had a negative relationship to birch cover (Delphacidae, Braconidae, Schizophora in pitfalls; Figure 2.5). We had very few transects with birch cover >25% and therefore some of our model estimates give wide prediction intervals of arthropod responses above 25% cover.

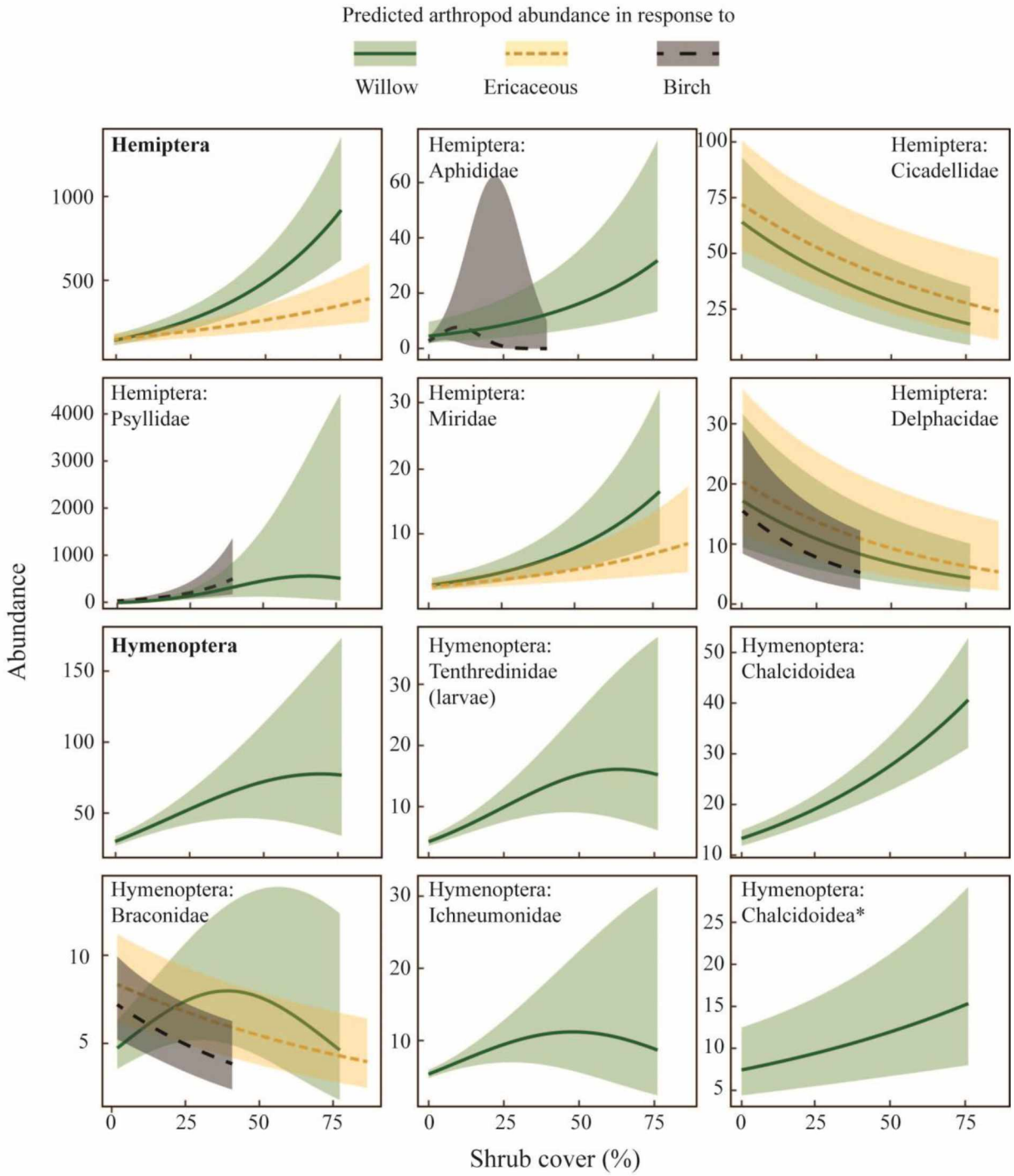

Figure 2.5 Taxon-specific responses to willow, ericaceous, and birch cover. Envelopes are 95% prediction intervals from the best-fit model. Wide prediction intervals at high shrub cover result from high variance in arthropod response and few observations of shrub cover above 50%. Asterisk (*) indicates counts analyzed from pitfall traps. Orders are in bold typeface. Predictors not included in the final model are not shown.

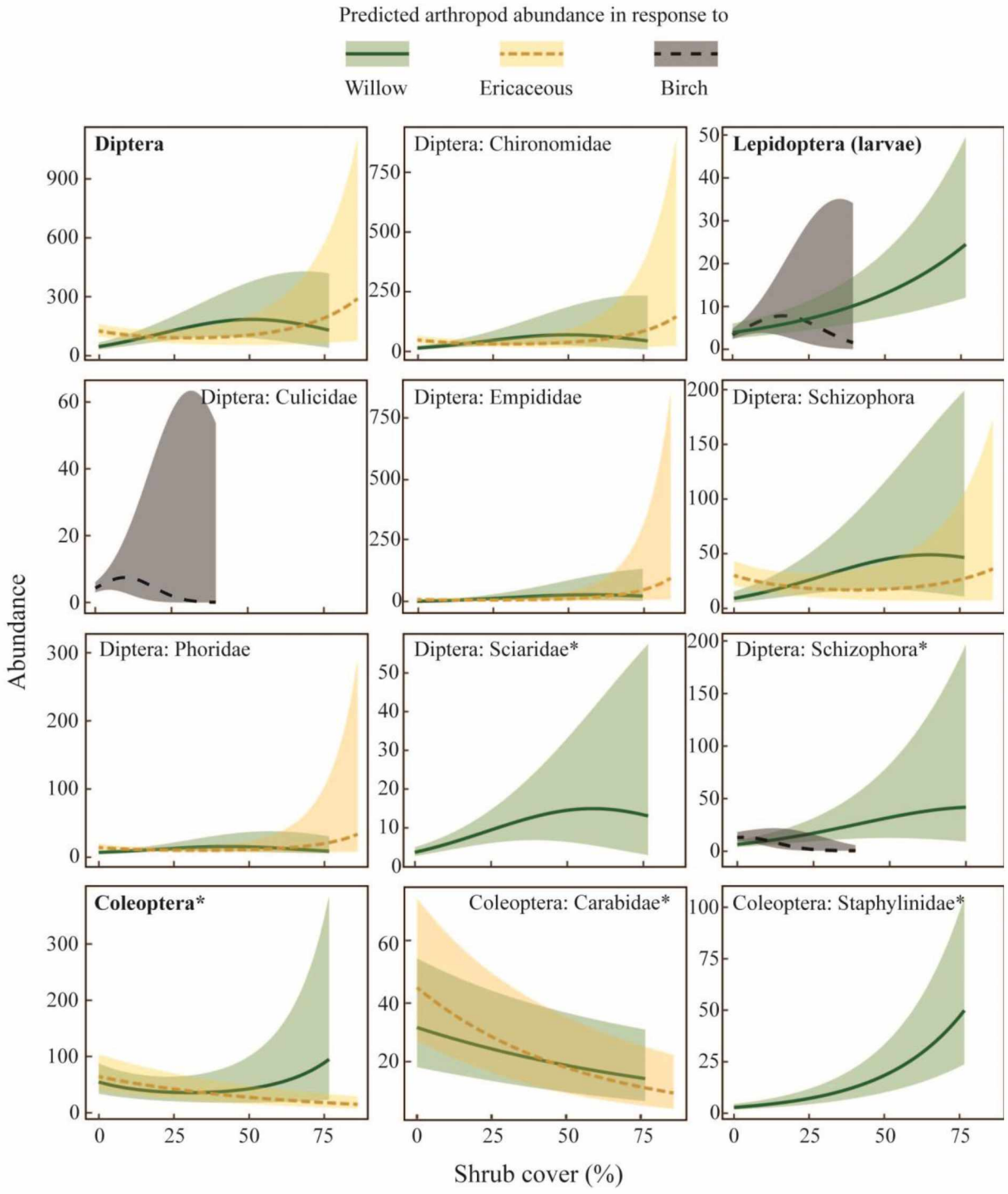

Figure 2.5, continued

There was some consistency among taxa in their response to slope when this variable was in the final model. Arthropod abundance tended to decrease on steep slopes. North-facing aspect and east-facing aspect were sometimes positively and sometimes negatively associated with abundance, with no clear pattern. See Table 2-C.2 in Appendix 2-C for coefficients and significance of the final model for each group shown in Figure 2.5.

Plot and site were included as random effects in all models. Including year as a random effect improved model fit ($\Delta AIC \geq 2$) for five families (Culicidae, Empididae, Sciaridae, Aphididae, Braconidae) (Table 2-C.2 in Appendix 2-C). Among the remaining taxa, including year either did not improve model fit, worsened model fit or hindered convergence and so it was dropped.

2.4.4 Diversity

Measures of taxonomic diversity were more strongly influenced by vegetation than by abiotic variables. For pitfall samples, richness and diversity increased with willow cover, but evenness was not significantly related to willow cover. Richness was greatest at intermediate ericaceous cover (40-50%) and diversity was greatest at intermediate ericaceous height (5-10 cm). All three measures of taxonomic diversity were greatest at intermediate birch height (10-20 cm). The highest richness and diversity were found on east-facing aspects, and the highest evenness on south-facing aspects (Table 2.3). For sweep-net samples richness was highest at intermediate willow height (80-100 cm), evenness decreased with willow cover, and diversity was not significantly related to either willow variable (Table 2.3). Both evenness and diversity decreased with ericaceous cover, while birch cover was positively associated with evenness. Richness was greatest at intermediate birch height (10-20 cm) and diversity at intermediate birch cover (~10%). Diversity was highest on south-facing aspects. See Tables 2-C.6 – 2-C.8 in Appendix 2-C for candidate models and

associated AIC values, and Table 2-C.9 in Appendix 2-C for coefficients and *P*-values associated with the models shown in Table 2.3.

Table 2.3 Linear mixed effects model selection results for taxonomic richness, evenness, and diversity of arthropods collected in pitfall traps and sweep-net samples during summer in 2015 and 2016 in northwestern Alaska, USA. Significant relationships are indicated as: (+) = positive, (-) = negative, (∩) = concave (∪) = convex . (0) indicates predictor not in final model. Site and plot were included as random effects in all models. Predictors eliminated from all final models are not shown (e.g., slope).

Sample type	Predictor	Richness	Evenness	Diversity
Pitfall	Willow cover	(+)	(0)	(+)
	Ericaceous cover	(∩)	(0)	(0)
	Ericaceous height	(0)	(0)	(∩)
	Birch height	(∩)	(∩)	(∩)
	N aspect	(0)	(-)	(0)
	E aspect	(+)	(0)	(+)
Sweep-net	Willow cover	(0)	(-)	(0)
	Willow height	(∩)	(0)	(0)
	Ericaceous cover	(0)	(-)	(-)
	Birch cover	(0)	(+)	(∩)
	Birch height	(∩)	(0)	(0)
	N aspect	(0)	(0)	(-)

2.4.5 Community Composition

Arthropod community composition was influenced strongly by both willow cover and height in our NMDS analysis. Permutation tests of correlation coefficients indicate that willow cover ($r^2 = 0.26$, $P = 0.001$), willow height ($r^2 = 0.18$, $P = 0.004$), and ericaceous height ($r^2 = 0.11$, $P = 0.023$) were significantly associated with changes in community composition of arthropods caught in pitfall traps, but birch cover, birch height, and ericaceous cover were not (Figure 2.6). Willow cover ($r^2 = 0.38$, $P = 0.001$) and willow height ($r^2 = 0.36$, $P = 0.001$) were significantly associated with changes in arthropod community composition in sweep net samples while birch and ericaceous variables were not (Figure 2.7), although ericaceous cover was nearly

significant ($r^2 = 0.12$, $P = 0.054$). Clustering of points within each plot (not shown) and plots within each site, even across years, indicated a high degree of spatial correlation, particularly among arthropods caught in pitfall traps (Figure 2.6). Willow cover and height strongly covaried in their influence on arthropod community composition, but this was not the case for birch or ericaceous shrubs (Figures 2.6 & 2.7).

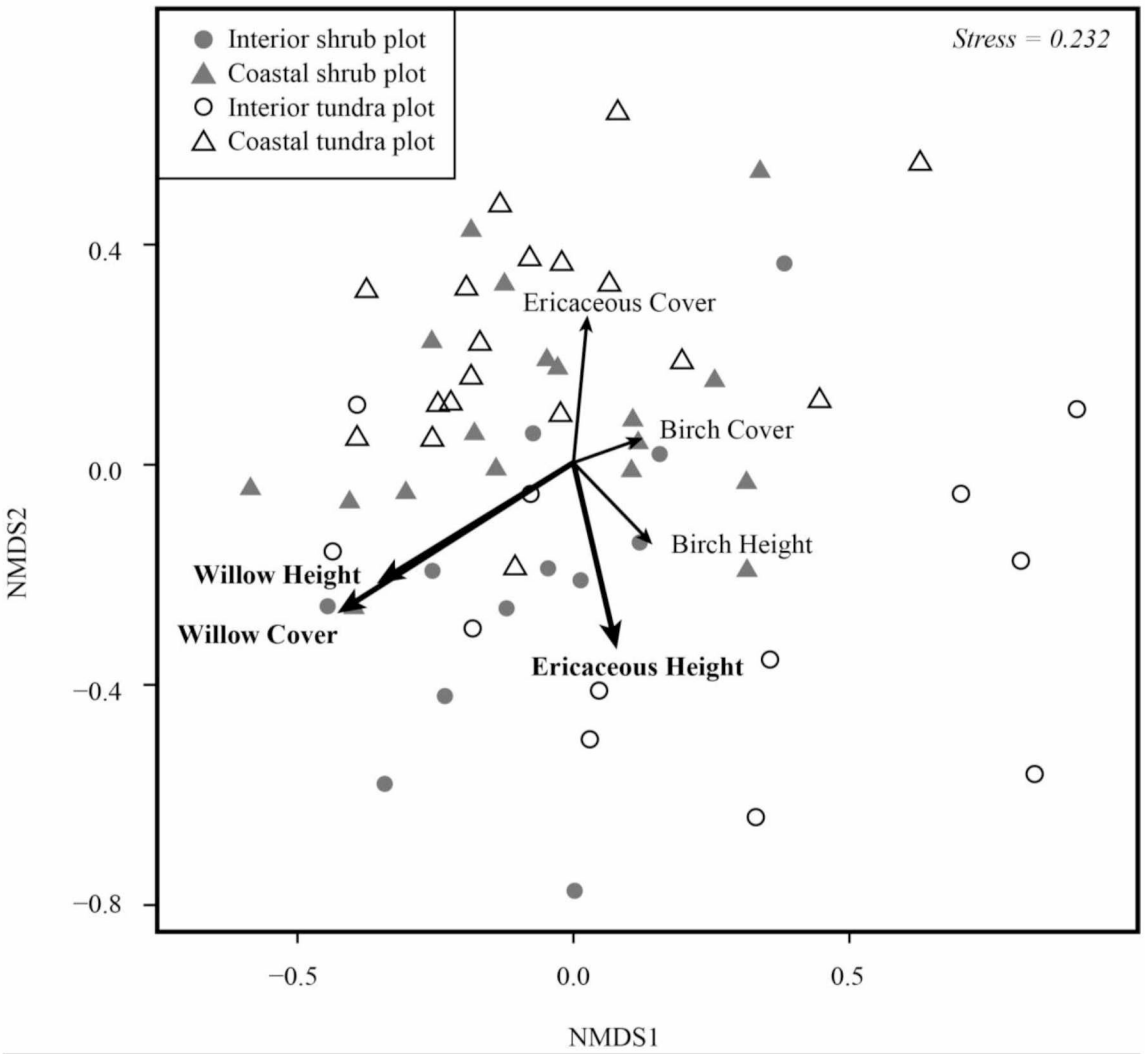

Figure 2.6 NMDS ordination results for arthropods caught in pitfall traps. Points represent a single collection point in a single year and are shaded by plot type with symbol indicating study site (coastal vs. interior). Axis 1 is primarily associated with willow cover/height and birch cover, axis 2 is associated with ericaceous cover and height. Vectors showing correlation between shrub variables and community composition are overlaid with length corresponding to significance.

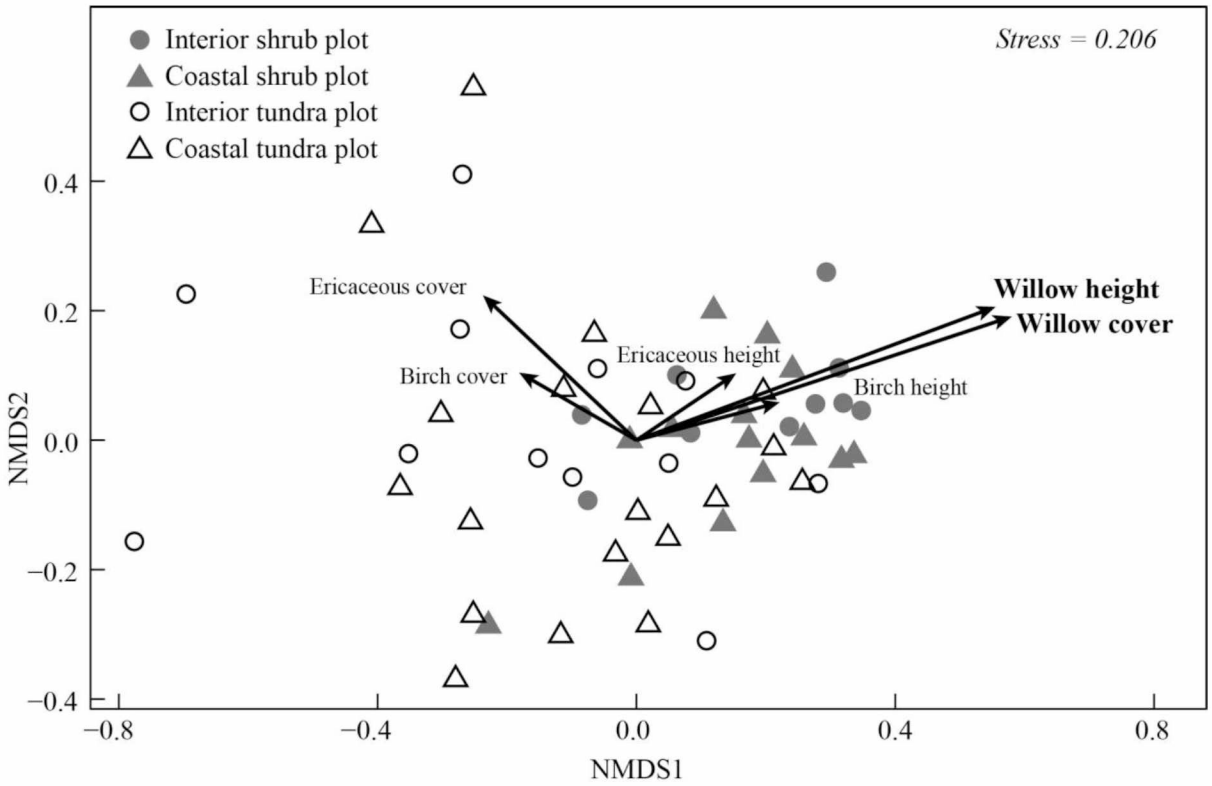

Figure 2.7 NMDS ordination results for arthropods caught in sweep-nets. Points represent a single collection point in a single year and are shaded by plot type with symbol indicating study site (coastal vs. interior). Axis 1 is primarily associated with willow cover/height and birch cover, axis 2 is associated with ericaceous cover. Vectors showing correlation between shrub variables and community composition are overlaid with length corresponding to significance.

2.5 DISCUSSION

Our results suggest that expansion of woody shrubs into tundra-dominated habitats has the potential to alter Arctic food webs and biodiversity by increasing the abundance and biomass of arthropods, especially herbivores. Shrub species varied greatly in their influence on arthropod communities, supporting our first hypothesis. Tall willows (*Salix alaxensis, S. glauca, S. pulchra, S. richardsonii*) had a positive or positive-curvilinear relationship with overall abundance, biomass of canopy-dwelling insects, abundance of most taxonomic groups, and taxonomic richness and diversity of ground-dwelling arthropods, and had the greatest influence of all vegetative or physiographic characteristics on both ground-dwelling and canopy-dwelling

arthropod community composition. Neither birch (*Betula nana* and *B. glandulosa*) nor ericaceous shrubs were found to have such a consistently strong effect. Our results clearly demonstrate that potential ecological effects of shrub expansion will depend on which shrub species are expanding most rapidly within a particular region.

Willow, birch, and ericaceous shrubs offer different resources to herbivores and pollinators, and as we hypothesized, this was reflected in the response of different trophic levels of arthropods. Of the taxa we identified, 71% of herbivores (Hemiptera: Aphididae, Psyllidae, Miridae; Lepidoptera larvae; and Hymenoptera: Tenthredinidae larvae) and 100% of parasitoids (Hymenoptera: Braconidae, Ichneumonidae, and Chalcidoidea) that use these herbivores as hosts had the highest abundances at moderate to high levels (>40%) of willow cover. Willow is preferred by a greater variety of vertebrate and invertebrate herbivores than birch or ericaceous shrubs (MacLean and Jensen 1985, Mulder 1999), so the palatability of this shrub species may explain the observed increases in herbivorous arthropods and associated parasitoids. In this study, at least 28% of individual arthropods identified were herbivorous and strongly associated with increased willow cover, so increased abundance of this trophic group alone could have a major influence on overall arthropod abundance, which could explain the increase in canopy-dwelling abundance and biomass of arthropods found in studies from other areas of Arctic Alaska (Rich et al. 2013).

Increased woody vegetation, coupled with higher air temperatures, could increase the abundance of herbivorous insects and rates of damage to plants. In the present study, we observed that most herbivorous taxa were positively associated with shrub cover. In a well-studied plant fossil record spanning 6 million years in present-day Wyoming, increased air temperatures were associated with increased rates of herbivory and a greater diversity of foliar

damage (Currano et al. 2008). Similar patterns have been found in high-latitude ecosystems (Labandeira and Currano 2013), including Svalbard (Wappler and Denk 2011). There is evidence from the present day that warmer air temperatures in forests are associated with increased intensity of insect outbreaks and range extensions of pests (Logan et al. 2003). Shrub expansion, coupled with projected increases in Arctic air temperature, may facilitate increased populations and expanded ranges of herbivorous insects in the Arctic.

Four groups of pollinators (Diptera: Culicidae, Chironomidae, Empididae, and Schizophora) (Kevan 1972, Lundgren and Olesen 2005, Tiusanen et al. 2016) were sufficiently abundant for individual analysis, and all but mosquitoes (Culicidae) were positively associated with ericaceous shrubs. Most of the flowering plants in our tundra plots were heathers (Ericaceae) and avens (*Dryas* spp.), flowers that are known to be pollinated by these three groups (Lundgren and Olesen 2005, Tiusanen et al. 2016), whereas shrub areas contained many shade-tolerant forbs such as fireweed (*Chamerion angustifolium*) and buttercup (*Ranunculus* spp.) (Swanson et al. 1985), which are pollinated by bees (Apidae), syrphid flies (Syrphidae), small beetles (Cantharidae and Staphylinidae), and muscid flies (Schizophora) (Schmid-Hempel and Speiser 1988, Steinbach and Gottsberger 1994, Lundgren and Olesen 2005). Willow itself is a source of nectar and pollen for arthropods, especially bees (Kevan 1972), and in Greenland willow catkins are visited by mosquitoes (Culicidae), dance flies (Empididae), and muscid flies (Schizophora) (Lundgren and Olesen 2005). Unlike willow and ericaceous shrubs, birch and alder shrubs are wind-pollinated and offer no resources to pollinators. In this study, we were not able to examine the impact of alder or high levels of birch cover but we postulate that an increase in these shrub types would negatively impact pollinators, unless these shrubs are associated with forbs beneficial to pollinators.

Given that the relative increase of willow, birch, alder, and ericaceous shrubs varies across the Arctic (Myers-Smith et al. 2011, Elmendorf et al. 2012), we expect that changes in arthropod communities relative to future shrub expansion will be heterogeneous in space. The greatest increase in arthropod abundance and benefits to insectivores may occur in areas where willow is responsible for most of the increase in woody vegetation, such as western Canada and Arctic Russia (Myers-Smith et al. 2011). Some pollinators may benefit from this increase in willow and associated forbs, but many that are dependent on ericaceous shrubs and other tundra-associated flowering species may be negatively impacted. We suspect that pollinators are negatively impacted where wind-pollinated birch and alder are expanding, such as Arctic Alaska.

We observed a curvilinear relationship to willow in many groups, with abundance peaking at about 50–60% cover. This suggests that expansion of shrubs onto tundra may increase abundance of these arthropod groups up to a certain point, but in very dense shrubs, abundance may decline. We did not have many observations of shrub cover exceeding 60%, leading to uncertainty in predictions in this range, but we suspect that the center of shrub thickets may be less suitable habitat for many arthropods than edges due to reduced solar radiation, reduced plant diversity, and the retention of snow, which can delay green-up and soil thaw and thus arthropod development (Post and Pedersen 2008, Myers-Smith et al. 2011, Sweet et al. 2014).

Shrub cover variables were better predictors of total abundance and biomass than height variables were, in contrast to our prediction that vertical area would drive increased abundance. This supports findings from grassland and low-shrub systems that plant species composition may be a more important determinant of arthropod community structure than structural characteristics of vegetation (Koricheva et al. 2000, Schaffers et al. 2008) but contrasts with findings from forest systems showing that structural characteristics are important drivers of arthropod

community structure (Halaj et al. 2000). It is important to consider, however, that both pitfall and sweep-net samples collected arthropods in a two-dimensional swath of habitat, regardless of vegetation height. If we had measured arthropod abundance and diversity per volume of vegetation, shrub height may have been a more important determinant than was evident in our study. Our key finding, however, was that the species composition of the shrubs was the most important predictor of arthropod abundance and biomass. Although deciduous shrubs have similar structural characteristics (tall, dense, shade-providing), grouping these plants in analyses may obscure their ecological relationships with other organisms, as demonstrated in our work and a recent analysis of plant-plant interactions among Arctic shrubs (Saccone et al. 2017).

Our results show that the ecological effects resulting from shrub expansion will depend greatly on which shrub species expand most rapidly, and we caution against ignoring ecology and trophic relationships when grouping arthropods or shrubs taxonomically. We provide support for the hypothesis that arthropod abundance and diversity will not respond identically to all shrub species, and we present evidence that tall willows exert a strong influence on arthropod community composition. Taken together, these results suggest that an increase in the cover of tall willow in Arctic tundra could alter food-web structure by increasing the abundance of herbivores and parasitoids, increasing prey availability for insectivores, and changing resources for pollinators. These will likely result in cascading effects across the ecosystem.

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2.7 APPENDICES

Appendix 2-A

Arthropod Abundance and Biomass

Table 2-A.1 Taxonomic identifications of arthropods collected on the Seward Peninsula, AK, during summers 2015 and 2016 via pitfall traps and sweep-netting.

ORDER	Family[1]	Guild(s)	Total	%	% in pitfalls[2]
ARANEAE		Predator	5189	13.14	92
CHILOPODA		Predator	257	0.65	100
COLEOPTERA			3671	9.29	97
	Unknown adults		40	0.10	100
	Byrrhidae	Herbivore	1	0.00	100
	Cantharidae	Predator, pollinator	72	0.18	13
	Carabidae	Predator, few herbivore	2216	5.61	100
	Chrysomelidae	Herbivore	9	0.02	78
	Coccinellidae	Predator, few herbivore	4	0.01	25
	Cryptophagidae	Fungivore, Detritivore	12	0.03	100
	Curculionidae	Herbivore	251	0.63	94
	Elateridae	Herbivore	113	0.29	98
	Latridiidae	Fungivore	44	0.11	95
	Leiodidae	Fungivore	83	0.21	99
	Silphidae	Scavenger, Herbivore	19	0.05	100
	Scarabaeidae	Varies within Family	8	0.02	100
	Staphylinidae	Predator	685	1.73	100
	Tenebrionidae	Detritivore, Fungivore	1	0.00	100
	Unknown larvae	Varies	115	0.29	82
DIPTERA			8588	21.74	30
	Bibionidae	Pollinator	17	0.04	6
	Cecidomyiidae	Gall-makers, Herbivore	219	0.56	75
	Ceratopogonidae	Pollinator, Blood-sucker	305	0.77	5
	Chironomidae	Non-feeding, larvae scavengers	2300	5.82	5
	Culicidae	Pollinator, Blood-sucker	501	1.27	7
	Mycetophilidae	Fungivore	228	0.58	84
	Sciaridae	Non-feeding, larvae fungivorous	692	1.75	73
	Simuliidae	Pollinator, Blood-sucker	210	0.53	26
	Tipulidae	Omnivore	196	0.50	81
	Dolichopodidae	Predator	100	0.25	9

Table 2-A.1, cont.

ORDER	Family[1]	Guild(s)	Total	%	% in pitfalls[2]
DIPTERA (cont.)	Empididae	Predator, Pollinator	717	1.81	4
	Phoridae	Varies within Family	529	1.34	39
	Pipunculidae	Parasitoid	93	0.24	6
	Rhagionidae	Predator	15	0.04	27
	Syrphidae	Pollinator	47	0.12	2
	Tabanidae	Pollinator, Blood-sucker	3	0.01	0
	Schizophora	Varies	2358	5.97	42
	Unknown larvae		34	0.09	29
EPHEMEROPTERA	adults	Non-feeding, larvae detritivorous	3	0.01	0
HEMIPTERA			16626	42.09	6
	Aphididae	Herbivore	775	1.96	14
	Cicadellidae	Herbivore	4882	12.36	13
	Coccoidea	Herbivore	14	0.04	65
	Delphacidae	Herbivore	1208	3.06	9
	Lygaeoidea	Herbivore	31	0.08	6
	Miridae	Herbivore, few predator	836	2.12	8
	Nabidae	Predator	84	0.21	5
	Psyllidae	Herbivore	8757	22.17	0
	Saldidae	Predator	14	0.04	100
	Tingidae	Herbivore	7	0.02	100
	Unknown	Varies	18	0.04	71
HYMENOPTERA			4293	10.87	38
	Tenthredinidae (larvae)	Herbivore	488	1.23	6
	Tenthredinidae (adult)	Predator	115	0.29	14
	Apidae	Pollinator	57	0.14	100
	Bethylidae	Parasitoid	1	0.00	100
	Braconidae	Parasitoid	576	1.46	32
	Diapriidae	Parasitoid	196	0.50	81
	Dryinidae	Parasitoid	21	0.05	38
	Ichneumonidae	Parasitoid	680	1.72	35
	Megaspilidae	Parasitoid	9	0.02	0
	Proctotrupidae	Parasitoid	7	0.02	58
	Scelionidae	Parasitoid	3	0.01	100
	Vespidae	Predator, pollinator	21	0.05	95
	Chalcidoidea	Parasitoid	1970	4.99	41
	Cynipoidea	Gall-makers	77	0.19	44
	Unknown larvae	Varies	4	0.01	100

Table 2-A.1, cont.

ORDER	Family[1]	Guild(s)	Total	%	% in pitfalls[2]
LEPIDOPTERA			601	1.52	9
	Larvae	Herbivore, few predator	444	1.12	10
	Adults	Pollinators	157	0.40	6
NEUROPTERA		Predator	28	0.07	0
ORTHOPTERA		Varies	3	0.01	0
PLECOPTERA		Non-feeding, larvae omnivorous	13	0.03	8
PSOCOPTERA		Fungivore	66	0.17	10
SIPHONAPTERA		Parasite	6	0.02	83
TRICHOPTERA		Pollinator/non-feeding, larvae detritivores	8	0.02	13
Soil-dwelling invertebrates & microarthropods not used in analysis					
ACARI[3]		Most fungivore or detritivore	59%		
ANNELIDA		Detritivore	58	0.15	100
COLLEMBOLA[3]		Detritivore	80%		
DECAPODA		Omnivore	1	0	100
GASTROPODA		Herbivore	91	0.23	100
THYSANOPTERA[3]		Fungivore, Herbivore	10%		
TOTAL			39503		

[1]Names listed in italices are superfamilies.

[2]Percentage of individuals from a particular taxon (e.g., Araneae) that were collected via pitfall trap vs. sweep-net. A value of 100 indicates that all individuals from that taxa were found in pitfall traps, a value of 0 indicates all individuals were collected via sweep-net.

[3]These orders do not have exact counts. Values reported are the % of samples where present.

Table 2-A.2 Biomass of arthropods collected on the Seward Peninsula, AK, during summers 2015 and 2016 via pitfall traps and sweep-netting. Each taxonomic group was weighed separately by life stage if multiple life stages were abundant, and by size class if size was highly variable. Any taxa caught frequently in both sample types was weighed separately for each sample type, since these may represent different species assemblages. Minute taxa (e.g. chalcidoidea, <2mm) were not measured as these represent a very small fraction of overall biomass.

Sample Type	Order	Taxon	Dry biomass (mg) [1]	N (if < 30)
Pitfall	Araneae	Araneae	6.33	
Pitfall	Araneae	Araneae_eggsac	7.29	
Pitfall	Araneae	Araneae_juv	0.15	
Pitfall	Coleoptera	Carabidae	21.72	
Pitfall	Coleoptera	Carabidae_lrg	75.09	
Pitfall	Coleoptera	Carabidae_med	16.60	
Pitfall	Coleoptera	Chrysomelidae	8.20	1
Pitfall	Coleoptera	Coleoptera_larvae	6.82	8
Pitfall	Coleoptera	Cryptophagidae	0.25	8
Pitfall	Coleoptera	Curculionidae	3.33	
Pitfall	Coleoptera	Elateridae	4.20	
Pitfall	Coleoptera	Latridiidae	0.19	
Pitfall	Coleoptera	Leiodidae	0.49	18
Pitfall	Coleoptera	Scarabaeidae	3.10	2
Pitfall	Coleoptera	Silphidae	15.10	2
Pitfall	Coleoptera	Staphylinidae	0.89	
Pitfall	Diptera	Carabidae_small	6.99	
Pitfall	Diptera	Cecidomyidae	0.02	
Pitfall	Diptera	Chironomidae	0.07	
Pitfall	Diptera	Culicidae	0.51	9
Pitfall	Diptera	Dolichopodidae	0.93	6
Pitfall	Diptera	Empididae	0.54	12
Pitfall	Diptera	Mycetophilidae	0.30	21
Pitfall	Diptera	Phoridae	0.10	
Pitfall	Diptera	Schizophora_lrg	10.23	10
Pitfall	Diptera	Schizophora_med	2.05	
Pitfall	Diptera	Schizophora_small	0.64	
Pitfall	Diptera	Sciaridae	0.05	

Table 2-A.2, cont.

Sample Type	Order	Taxon	Dry biomass (mg) [1]	N (if < 30)
Pitfall	Diptera	Simuliidae	0.26	
Pitfall	Diptera	Syrphidae	3.00	3
Pitfall	Diptera	Tipulidae_pupa	12.20	1
Pitfall	Diptera	Tipulidae_winged	4.33	16
Pitfall	Diptera	Tipulidae_wingless	13.67	14
Pitfall	Hemiptera	Aphidoidea	0.08	
Pitfall	Hemiptera	Cicadellidae_adult	0.48	
Pitfall	Hemiptera	Cicadellidae_nymph	0.12	
Pitfall	Hemiptera	Delphacidae_adult	0.39	13
Pitfall	Hemiptera	Delphacidae_nymph	0.13	12
Pitfall	Hemiptera	Psyllidae_adult	0.10	5
Pitfall	Hemiptera	Psyllidae_nymph	0.13	11
Pitfall	Hymenoptera	Tenthredinidae_adult	1.50	1
Pitfall	Hymenoptera	Tenthredinidae_larvae	1.50	2
Pitfall	Lepidoptera	Lepidoptera_larvae	10.03	3
Sweep	Araneae	Araneae	2.11	
Sweep	Araneae	Araneae_juv	0.23	
Sweep	Coleoptera	Cantharidae	2.18	7
Sweep	Coleoptera	Carabidae_small	2.20	1
Sweep	Coleoptera	Chrysomelidae	2.50	1
Sweep	Coleoptera	Coleoptera_larvae	0.29	8
Sweep	Coleoptera	Curculionidae	0.79	8
Sweep	Coleoptera	Latridiidae	0.10	2
Sweep	Coleoptera	Staphylinidae	0.30	2
Sweep	Diptera	Bibionidae	3.00	1
Sweep	Diptera	Cecidomyidae	0.00	2
Sweep	Diptera	Ceratopogonidae	0.12	
Sweep	Diptera	Chironomidae	0.06	
Sweep	Diptera	Culicidae	0.78	
Sweep	Diptera	Dolichopodidae	1.23	
Sweep	Diptera	Empididae	0.36	
Sweep	Diptera	Mycetophilidae	0.25	13
Sweep	Diptera	Phoridae	0.12	
Sweep	Diptera	Pipunculidae	0.32	12

Table 2-A.2, cont.

Sample Type	Order	Taxon	Dry biomass (mg) [1]	N (if < 30)
Sweep	Diptera	Rhagionidae	2.15	4
Sweep	Diptera	Schizophora_lrg	4.20	4
Sweep	Diptera	Schizophora_med	1.70	
Sweep	Diptera	Schizophora_small	0.85	
Sweep	Diptera	Sciaridae	0.07	
Sweep	Diptera	Simuliidae	0.38	
Sweep	Diptera	Syrphidae	2.15	15
Sweep	Diptera	Tipulidae_winged	4.47	3
Sweep	Hemiptera	Aphidoidea	0.11	
Sweep	Hemiptera	Cicadellidae_adult	0.46	
Sweep	Hemiptera	Cicadellidae_nymph	0.19	
Sweep	Hemiptera	Coccoidea	1.80	1
Sweep	Hemiptera	Delphacidae_adult	0.61	
Sweep	Hemiptera	Delphacidae_nymph	0.21	
Sweep	Hemiptera	Lygaeoidea_adult	2.17	3
Sweep	Hemiptera	Lygaeoidea_nymph	0.67	3
Sweep	Hemiptera	Miridae_adult	0.69	
Sweep	Hemiptera	Miridae_nymph	0.44	
Sweep	Hemiptera	Psyllidae_adult	0.21	
Sweep	Hemiptera	Psyllidae_nymph	0.15	
Sweep	Hymenoptera	Ichneumonidae	0.36	
Sweep	Hymenoptera	Tenthredinidae_adult	1.36	
Sweep	Hymenoptera	Tenthredinidae_larvae	2.44	
Sweep	Lepidoptera	Lepidoptera_adult	0.76	
Sweep	Lepidoptera	Lepidoptera_larvae	2.13	
Sweep	Neuroptera	Neuroptera	0.76	12
Sweep	Orthoptera	Orthoptera	11.40	1
Sweep	Plecoptera	Plecoptera	0.80	1
Sweep	Psocoptera	Psocoptera	0.18	19
Sweep	Trichoptera	Trichoptera	2.00	3

[1]Biomass measured as average mass of 30 individuals (or N if < 30) dried at 40°C for 48 hours.

Appendix 2-B

Vegetation and Landscape Variables

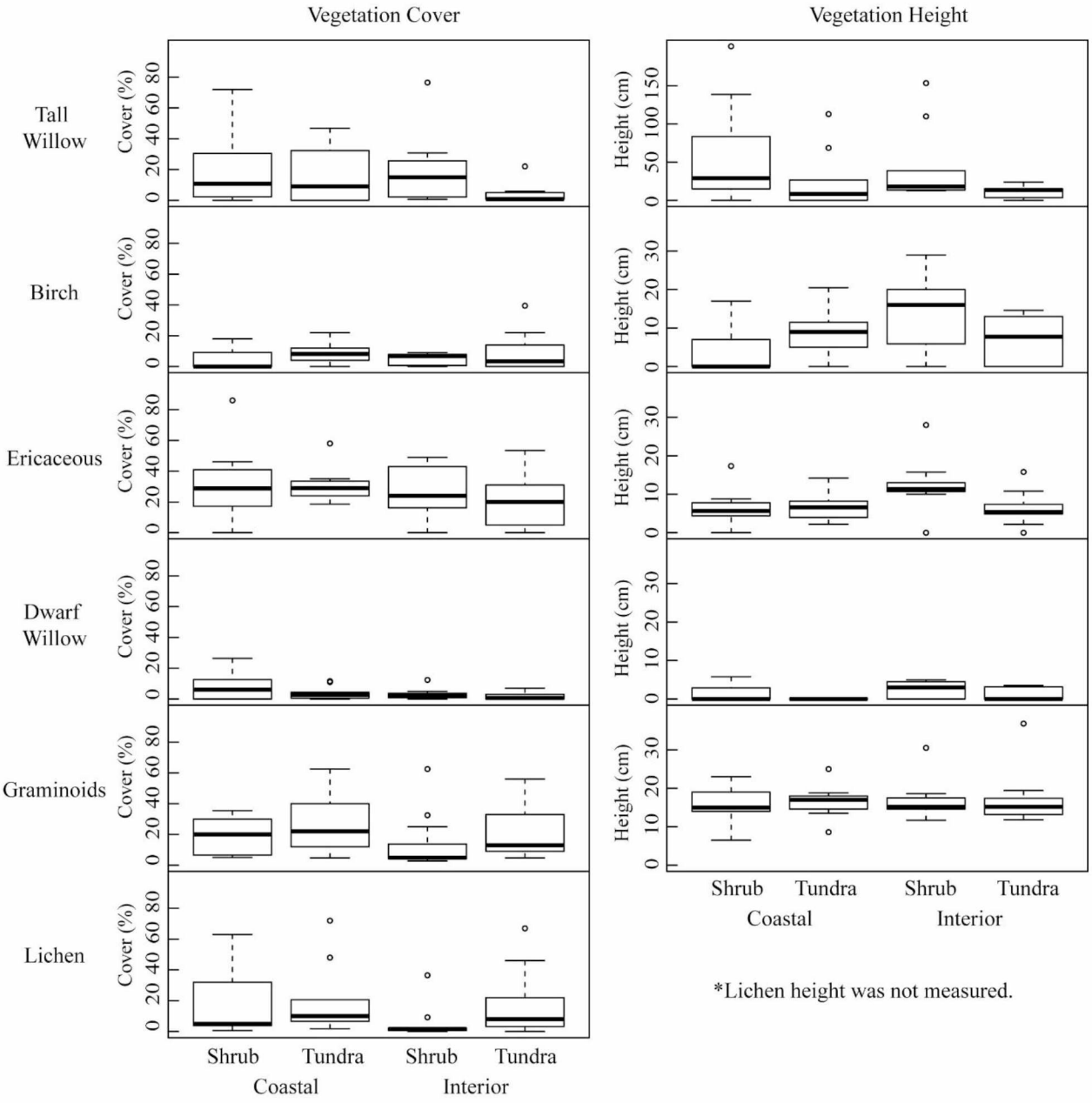

Figure 2-B.1 Vegetation characteristics used in model selection. Boxplots show median, 1st quantile, and 3rd quantile of each vegetation measurement on shrub-dominated and tundra-dominated plots at both study sites.

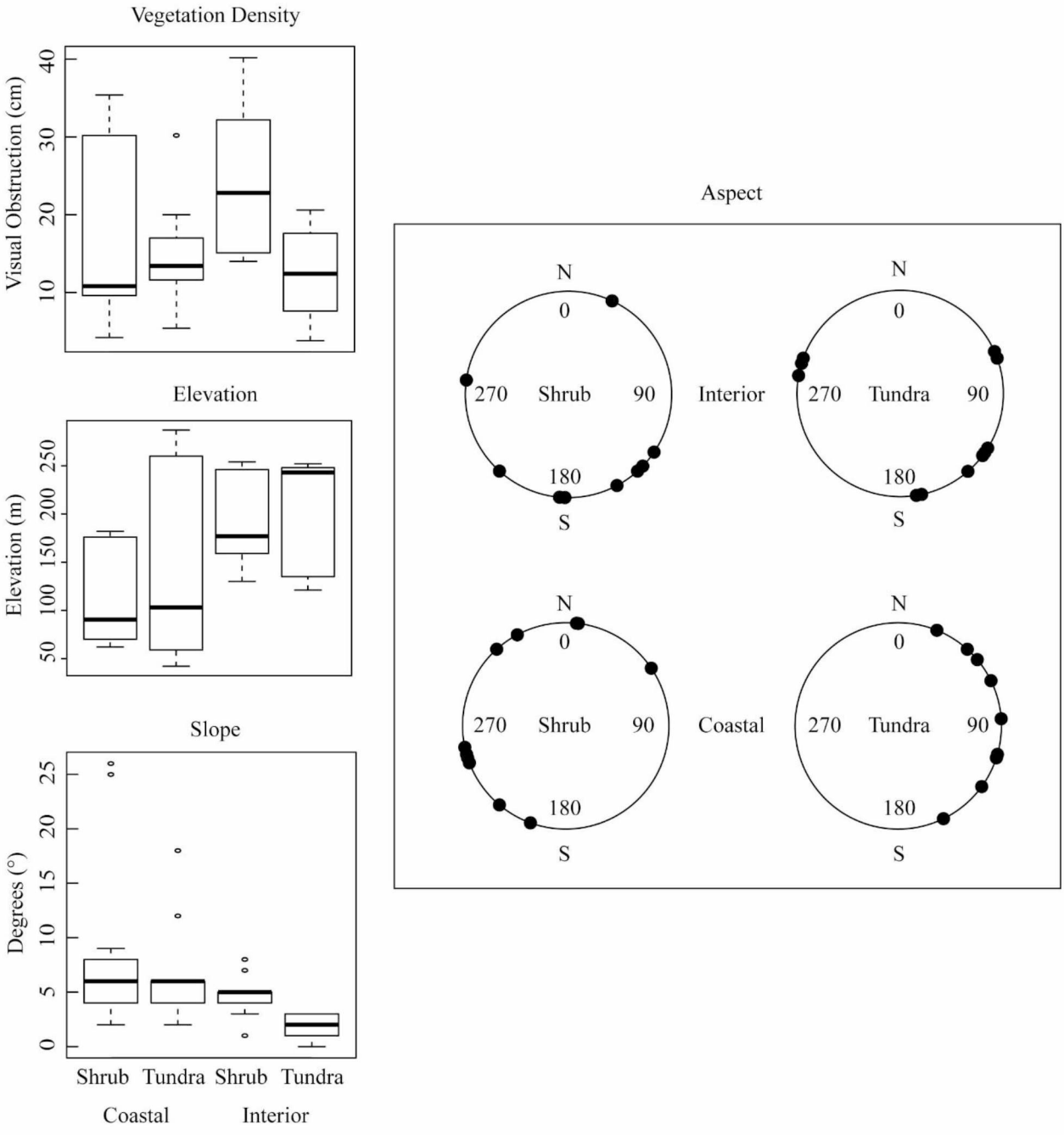

Figure 2-B.2 Landscape characteristics used in model selection. Boxplots show median, 1st quantile, and 3rd quantile of each variable on shrub-dominated and tundra-dominated plots at both study sites.

Appendix 2-C

Model Selection Procedure and Results

Table 2-C.1 Truncations made to variables used in model selection for overall abundance, overall biomass, taxon-specific abundance, and diversity of arthropods collected on the Seward Peninsula, AK, during summers 2015 and 2016.

Variable	Maximum	Truncated Maximum	Points Truncated
Hemiptera	1881	750	1
Aphidoidea	196	50	2
Psyllidae	1765	600	1
Slope	26	15	4
Willow Height	201.8	153	3
Birch Cover	39.5	22	1
Birch Height	96	39	2
Ericaceous Height	32.2	17	4

Table 2-C.2 Coefficients and *P*-values of parameters in final models for 6 orders (bold) and 20 families/life stages of arthropods collected on the Seward Peninsula, AK, during summers 2015 and 2016. Predictions for each model are shown in Figure 2.5.

Order	Family	Sample Type	Year[1]	Willow	*P*	Willow[2]	*P*	Dwarf Birch	*P*	Dwarf Birch[2]	*P*
Araneae		**pitfall**	**N**								
Coleoptera		**pitfall**	**N**	**-0.028**	**0.013**	**0.000**	**0.008**				
Coleoptera	Carabidae	pitfall	N	-0.105	0.097						
Coleoptera	Staphylinidae	pitfall	N	0.038	<0.001						
Diptera		**sweep**	**N**	**0.055**	**<0.001**	**-0.001**	**0.000**				
Diptera	Chironomidae	sweep	N	0.064	<0.001	-0.001	0.002				
Diptera	Culicidae	sweep	Y					0.112	0.055	-0.006	0.073
Diptera	Empididae	sweep	Y	0.080	<0.001	-0.001	0.002				
Diptera	Phoridae	sweep	N	0.080	<0.001	-0.001	0.000				
Diptera	Schizophora*	sweep	N	0.052	<0.001	0.000	0.011				
Diptera	Schizophora*	pitfall	N	0.047	<0.001	0.000	0.137	0.019	0.683	-0.004	0.063
Diptera	Sciaridae	pitfall	Y	0.048	<0.001	0.000	0.036				
Hemiptera		**sweep**	**N**	**0.011**	**0.011**						
Hemiptera	Aphidoidea	sweep	Y	0.026	0.001			0.204	0.004	-0.010	0.014
Hemiptera	Cicadellidae	sweep	N	-0.015	0.011						
Hemiptera	Delphacidae	sweep	N	-0.019	0.017			-0.029	0.081		
Hemiptera	Miridae	sweep	N	0.026	<0.001						
Hemiptera	Psyllidae	sweep	N	0.101	<0.001	-0.001	0.006	0.057	0.010		
Hymenoptera		**sweep**	**N**	**0.027**	**<0.001**	**0.000**	**0.060**				
Hymenoptera	Tenthredinidae (larvae)	sweep	N	0.042	<0.001	0.000	0.010				
Hymenoptera	Braconidae	sweep	Y	0.028	0.001	0.000	0.002	-0.016	0.100		
Hymenoptera	Chalcidoidea*	sweep	N	0.015	<0.001						
Hymenoptera	Chalcidoidea*	pitfall	N	0.009	0.065						
Hymenoptera	Ichneumonidae	pitfall	N	0.031	0.005	0.000	0.053				
Lepidoptera		**sweep**	**N**	**0.013**	**0.024**						
Lepidoptera	(larvae only)	sweep	N	0.024	0.001			0.101	0.025	-0.003	0.044

Table 2-C.2, cont.

Order	Family	Ericaceous	*P*	Ericaceous[2]	*P*	North	*P*	East	*P*	Slope	*P*
Araneae						**-0.228**	**0.005**				
Coleoptera		**-0.017**	**0.001**							**-0.057**	**0.005**
Coleoptera	Carabidae	-0.019	0.017							-0.086	0.002
Coleoptera	Staphylinidae										
Diptera		**-0.022**	**0.038**	**0.000**	**0.008**	**0.246**	**0.007**				
Diptera	Chironomidae	-0.029	0.035	0.000	0.008	0.272	0.037				
Diptera	Culicidae										
Diptera	Empididae	-0.025	0.147	0.001	0.007	0.524	0.001	0.464	0.002	-0.089	0.003
Diptera	Phoridae	-0.038	0.020	0.001	0.008					-0.070	0.021
Diptera	Schizophora*	-0.029	0.051	0.000	0.032					-0.043	0.029
Diptera	Schizophora*							0.235	0.068		
Diptera	Sciaridae							0.339	0.018	-0.046	0.062
Hemiptera		**0.024**	**<0.001**								
Hemiptera	Aphidoidea										
Hemiptera	Cicadellidae	-0.012	0.060								
Hemiptera	Delphacidae	-0.016	0.074							-0.081	0.034
Hemiptera	Miridae	0.016	0.026								
Hemiptera	Psyllidae					-0.332	0.084				
Hymenoptera											
Hymenoptera	Tenthredinidae (larvae)					-0.257	0.012				
Hymenoptera	Braconidae	-0.009	0.042					-0.192	0.062		
Hymenoptera	Chalcidoidea*										
Hymenoptera	Chalcidoidea*										
Hymenoptera	Ichneumonidae										
Lepidoptera						**-0.328**	**0.038**	**-0.272**	**0.084**		
Lepidoptera	(larvae only)					-0.416	0.023	-0.357	0.054		

[1]Indicates if year, as well as site and plot, was included as a random effect.
*These families analyzed for both pitfall and sweep-net samples, since they were abundant in both sample types and likely represent different species assemblages.

Table 2-C.3 AIC model selection between cover and height variables for each shrub type used in modeling abundance, biomass, and diversity of arthropods collected on the Seward Peninsula, AK, during summers 2015 and 2016. Results used to create the full models used in model selection procedures shown in Table 2-C.4-2.13. Vegetation variables (e.g., EricaceousCover) included a linear and quadratic term. All models included aspect and slope as fixed effects, and study site and plot as random effects.

Sample Type	Response	Predictors	Year incl?	AIC	AICc	k	log-likelihood
Pitfall	Abundance	EricaceousCover + BirchHeight + TallWillowCover	Y	760.0	767.9	14	-366.01
Pitfall	Abundance	EricaceousCover + BirchCover + TallWillowCover	Y	761.8	769.7	14	-366.92
Pitfall	Abundance	EricaceousCover + BirchCover + TallWillowHeight	Y	764.4	772.3	14	-368.20
Pitfall	Abundance	EricaceousHeight + BirchCover + TallWillowCover	Y	765.7	773.6	14	-368.84
Sweep	Abundance	EricaceousCover + BirchHeight + TallWillowCover	N	811.6	819.2	13	-392.82
Sweep	Abundance	EricaceousCover + BirchCover + TallWillowCover	N	814.5	822.1	13	-394.25
Sweep	Abundance	EricaceousHeight + BirchCover + TallWillowCover	N	820.1	827.7	13	-397.04
Sweep	Abundance	EricaceousCover + BirchCover + TallWillowHeight	N	821.0	828.6	13	-397.48
Pitfall	√Biomass	EricaceousCover + BirchCover + TallWillowCover	N	495.5	502.2	13	-234.77
Pitfall	√Biomass	EricaceousCover + BirchHeight + TallWillowCover	N	495.6	502.3	13	-234.80
Pitfall	√Biomass	EricaceousCover + BirchCover + TallWillowHeight	N	495.7	502.4	13	-234.86
Pitfall	√Biomass	EricaceousHeight + BirchCover + TallWillowCover	N	497.3	504.0	13	-235.64
Sweep	√Biomass	EricaceousCover + BirchHeight + TallWillowCover	N	285.6	293.2	13	-129.79
Sweep	√Biomass	EricaceousHeight + BirchCover + TallWillowCover	N	288.0	295.6	13	-131.02
Sweep	√Biomass	EricaceousCover + BirchCover + TallWillowCover	N	288.7	296.3	13	-131.33
Sweep	√Biomass	EricaceousCover + BirchCover + TallWillowHeight	N	294.6	302.2	13	-134.32
Pitfall	Richness	EricaceousCover + BirchHeight + TallWillowCover	Y	274.2	274.8	14	-123.11
Pitfall	Richness	EricaceousHeight + BirchCover + TallWillowCover	Y	280.7	281.2	14	-126.33
Pitfall	Richness	EricaceousCover + BirchCover + TallWillowCover	Y	280.9	281.5	14	-126.47
Pitfall	Richness	EricaceousCover + BirchCover + TallWillowHeight	Y	283.2	283.7	14	-127.59
Pitfall	Evenness	EricaceousCover + BirchHeight + TallWillowCover	N	-147.9	-147.3	13	86.93
Pitfall	Evenness	EricaceousCover + BirchCover + TallWillowHeight	N	-145.4	-144.9	13	85.69
Pitfall	Evenness	EricaceousCover + BirchCover + TallWillowCover	N	-143.6	-143.0	13	84.77
Pitfall	Evenness	EricaceousHeight + BirchCover + TallWillowCover	N	-142.4	-141.8	13	84.18

Table 2-C.3, cont.

Sample Type	Response	Predictors	Year incl?	AIC	AICc	k	log-likelihood
Pitfall	Diversity	EricaceousCover + BirchHeight + TallWillowCover	N	-6.7	-6.2	13	16.36
Pitfall	Diversity	EricaceousHeight + BirchCover + TallWillowCover	N	-1.5	-1.0	13	13.75
Pitfall	Diversity	EricaceousCover + BirchCover + TallWillowCover	N	1.8	2.3	13	12.11
Pitfall	Diversity	EricaceousCover + BirchCover + TallWillowHeight	N	2.5	3.0	13	11.77
Sweep	Richness	EricaceousCover + BirchHeight + TallWillowCover	N	273.8	281.4	13	-123.88
Sweep	Richness	EricaceousCover + BirchCover + TallWillowHeight	N	277.4	285.0	13	-125.70
Sweep	Richness	EricaceousHeight + BirchCover + TallWillowCover	N	279.5	287.1	13	-126.73
Sweep	Richness	EricaceousCover + BirchCover + TallWillowCover	N	280.8	288.4	13	-127.38
Sweep	Evenness	EricaceousCover + BirchCover + TallWillowCover	N	-80.6	-73.0	13	53.28
Sweep	Evenness	EricaceousHeight + BirchCover + TallWillowCover	N	-80.5	-72.9	13	53.25
Sweep	Evenness	EricaceousCover + BirchHeight + TallWillowCover	N	-77.4	-69.8	13	51.72
Sweep	Evenness	EricaceousCover + BirchCover + TallWillowHeight	N	-76.0	-68.4	13	50.99
Sweep	Diversity	EricaceousCover + BirchCover + TallWillowCover	N	27.3	34.9	13	-0.64
Sweep	Diversity	EricaceousHeight + BirchCover + TallWillowCover	N	29.6	37.2	13	-1.79
Sweep	Diversity	EricaceousCover + BirchHeight + TallWillowCover	N	31.6	39.2	13	-2.80
Sweep	Diversity	EricaceousCover + BirchCover + TallWillowHeight	N	31.6	39.2	13	-2.82

Table 2-C.4 Model selection for abundance of arthropods collected on the Seward Peninsula, AK, during summers 2015 and 2016. Final model shown in bold. Coefficients of each best-fitting model described in Table 2.2.

Sample Type	Predictor(s)	Year incl.?	AIC	AICc	k	log-likelihood
Pitfall	**EricaceousCover + TallWillowCover + Slope**	**Y**	**754.0**	**756.4**	**8**	**-368.99**
	EricaceousCover + BirchHeight + BirchHeight^2 + TallWillowCover + East + Slope	Y	755.0	759.7	11	-366.52
	EricaceousCover + BirchHeight + BirchHeight^2 + TallWillowCover + Slope	Y	755.7	759.6	10	-367.86
	EricaceousCover + EricaceousCover^2 + BirchHeight + BirchHeight^2 + TallWillowCover + East + Slope	Y	756.1	761.8	12	-366.04
	EricaceousCover + EricaceousCover^2 + BirchHeight + BirchHeight^2 + TallWillowCover + North + East + Slope	Y	758.0	764.7	13	-366.02
	EricaceousCover + EricaceousCover^2 + BirchHeight + BirchHeight^2 + TallWillowCover + TallWillowCover^2 + North + East + Slope	Y	760.0	767.9	14	-366.01
	Null Model	Y	778.1	779.1	5	-384.06
Sweep	**EricaceousCover + EricaceousCover^2 + TallWillowCover + TallWillowCover^2**	**N**	**805.4**	**805.7**	**8**	**-394.68**
	TallWillowCover	N	806.9	807.1	5	-398.47
	EricaceousCover + EricaceousCover^2 + TallWillowCover + TallWillowCover^2 + North	N	806.9	807.2	9	-394.50
	Null Model	N	806.9	808.0	5	-398.47
	TallWillowCover + TallWillowCover^2	N	807.1	807.3	6	-397.57
	EricaceousCover + EricaceousCover^2 + TallWillowCover + TallWillowCover^2 + North + East	N	808.9	809.3	10	-394.45
	EricaceousCover + EricaceousCover^2 + BirchHeight + BirchHeight^2 + TallWillowCover + TallWillowCover^2 + North + East	N	809.6	810.1	12	-392.82
	EricaceousCover + EricaceousCover^2 + BirchHeight + BirchHeight^2 + TallWillowCover + TallWillowCover^2 + North + East + Slope	N	811.6	819.2	13	-392.82

Table 2-C.5 Model selection for biomass (square-root transformed) of arthropods collected on the Seward Peninsula, AK, during summers 2015 and 2016. Final model shown in bold. Coefficients of each best-fitting model described in Table 2.2.

Sample Type	Predictor(s)	Year incl.?	AIC	AICc	k	log-likelihood
Pitfall	**East + Slope**	**N**	**488.0**	**488.2**	**6**	**-238.02**
	Null Model	N	489.3	490.0	4	-240.67
	EricaceousCover + East + Slope	N	489.4	489.7	7	-237.68
	EricaceousCover + TallWillowCover + East + Slope	N	490.5	490.8	8	-237.27
	EricaceousCover + TallWillowCover + TallWillowCover^2 + East + Slope	N	491.5	491.8	9	-236.74
	EricaceousCover + TallWillowCover + TallWillowCover^2 + North + East + Slope	N	492.2	492.6	10	-236.12
	EricaceousCover + EricaceousCover^2 + TallWillowCover + TallWillowCover^2 + North + East + Slope	N	493.3	493.7	11	-235.63
	EricaceousCover + EricaceousCover^2 + BirchCover + BirchCover^2 + TallWillowCover + TallWillowCover^2 + North + East + Slope	N	495.5	502.2	13	-234.77
Sweep	**BirchHeight + TallWillowCover**	**N**	**276.5**	**276.7**	**6**	**-132.26**
	BirchHeight + TallWillowCover + Slope	N	276.7	277.0	7	-131.34
	EricaceousHeight + EricaceousHeight^2 + BirchHeight + TallWillowCover + Slope	N	278.5	278.8	9	-130.26
	EricaceousHeight + EricaceousHeight^2 + BirchHeight + BirchHeight^2 + TallWillowCover + Slope	N	280.1	280.5	10	-130.05
	EricaceousHeight + EricaceousHeight^2 + BirchHeight + BirchHeight^2 + TallWillowCover + TallWillowCover^2 + Slope	N	281.7	282.1	11	-129.83
	EricaceousHeight + EricaceousHeight^2 + BirchHeight + BirchHeight^2 + TallWillowCover + TallWillowCover^2 + North + Slope	N	283.2	283.7	12	-129.62
	EricaceousHeight + EricaceousHeight^2 + BirchHeight + BirchHeight^2 + TallWillowCover + TallWillowCover^2 + North + East + Slope	N	285.1	292.7	13	-129.58
	Null Model	N	318.3	319.0	4	-155.14

Table 2-C.6 Model selection for richness (number of families) of arthropods collected on the Seward Peninsula, AK, during summers 2015 and 2016. Final model shown in bold.

Sample Type	Predictor(s)	Year incl.?	AIC	AICc	k	log-likelihood
Pitfall	**EricaceousCover + EricaceousCover^2 + BirchHeight + BirchHeight^2 + TallWillowCover + East**	**Y**	**270.5**	**270.9**	**11**	**-124.25**
	EricaceousCover + EricaceousCover^2 + BirchHeight + BirchHeight^2 + TallWillowCover + TallWillowCover^2 + East	Y	271.1	271.6	12	-123.57
	EricaceousCover + BirchHeight + BirchHeight^2 + TallWillowCover + East	Y	271.3	271.7	10	-125.66
	EricaceousCover + EricaceousCover^2 + BirchHeight + BirchHeight^2 + TallWillowCover + TallWillowCover^2 + North + East	Y	272.3	272.8	13	-123.13
	EricaceousCover + EricaceousCover^2 + BirchHeight + BirchHeight^2 + TallWillowCover + TallWillowCover^2 + North + East + Slope	Y	274.2	274.8	14	-123.11
	Null Model	Y	284.4	284.6	5	-137.19
Sweep	**BirchHeight + BirchHeight^2 + TallWillowHeight + TallWillowHeight^2**	**N**	**247.1**	**247.4**	**8**	**-115.52**
	BirchHeight + TallWillowHeight + TallWillowHeight^2	N	247.2	247.5	7	-116.62
	TallWillowHeight + TallWillowHeight^2	N	247.9	248.1	6	-117.96
	EricaceousHeight + EricaceousHeight^2 + BirchHeight + BirchHeight^2 + TallWillowHeight + TallWillowHeight^2 + Slope	N	248.2	248.6	11	-113.09
	EricaceousHeight + EricaceousHeight^2 + BirchHeight + BirchHeight^2 + TallWillowHeight + TallWillowHeight^2 + North + Slope	N	248.9	249.3	12	-112.44
	EricaceousHeight + BirchHeight + BirchHeight^2 + TallWillowHeight + TallWillowHeight^2	N	249.0	249.4	9	-115.52
	EricaceousHeight + EricaceousHeight^2 + BirchHeight + BirchHeight^2 + TallWillowHeight + TallWillowHeight^2	N	249.3	249.6	10	-114.63
	EricaceousHeight + EricaceousHeight^2 + BirchHeight + BirchHeight^2 + TallWillowHeight + TallWillowHeight^2 + North + East + Slope	N	**250.5**	251.0	13	-112.22
	Null Model	N	261.3	261.5	4	-126.67

Table 2-C.7 Model selection for evenness of families of arthropods collected on the Seward Peninsula, AK, during summers 2015 and 2016. Final model shown in bold.

Sample Type	Predictor(s)	Year incl.?	AIC	AICc	k	log-likelihood
Pitfall	**BirchHeight + BirchHeight^2 + North**	**N**	**-155.3**	**-155.0**	**7**	**84.63**
	EricaceousCover + BirchHeight + BirchHeight^2 + TallWillowHeight + TallWillowHeight^2 + North	N	-154.9	-154.5	10	87.46
	BirchHeight + BirchHeight^2	N	-154.6	-154.3	6	83.28
	BirchHeight + BirchHeight^2 + TallWillowHeight + TallWillowHeight^2 + North	N	-154.4	-154.0	9	86.19
	EricaceousCover + EricaceousCover^2 + BirchHeight + BirchHeight^2 + TallWillowHeight + TallWillowHeight^2 + North	N	-154.3	-153.9	11	88.16
	EricaceousCover + EricaceousCover^2 + BirchHeight + BirchHeight^2 + TallWillowHeight + TallWillowHeight^2 + North + Slope	N	-152.4	-151.9	12	88.18
	EricaceousCover + EricaceousCover^2 + BirchHeight + BirchHeight^2 + TallWillowHeight + TallWillowHeight^2 + North + East + Slope	N	-150.4	-149.9	13	88.18
	Null Model	N	-150.0	-149.8	4	78.98
Sweep	**EricaceousCover + BirchCover + TallWillowCover**	**N**	**-111.9**	**-111.7**	**7**	**62.97**
	EricaceousCover + BirchCover + BirchCover^2 + TallWillowCover	N	-111.0	-110.6	8	63.47
	EricaceousCover + TallWillowCover	N	-110.8	-110.5	6	61.38
	EricaceousCover + BirchCover + BirchCover^2 + TallWillowCover + TallWillowCover^2	N	-109.9	-109.6	9	64.00
	Null Model	N	-108.9	-108.7	4	58.43
	EricaceousCover + BirchCover + BirchCover^2 + TallWillowCover + TallWillowCover^2 + Slope	N	-108.4	-108.0	10	64.19
	EricaceousCover + EricaceousCover^2 + BirchCover + BirchCover^2 + TallWillowCover + TallWillowCover^2 + Slope	N	-106.6	-106.1	11	64.29
	EricaceousCover + EricaceousCover^2 + BirchCover + BirchCover^2 + TallWillowCover + TallWillowCover^2 + North + East + Slope	N	-106.4	-105.9	13	66.20
	EricaceousCover + EricaceousCover^2 + BirchCover + BirchCover^2 + TallWillowCover + TallWillowCover^2 + East + Slope	N	-104.6	-104.1	12	64.29

Table 2-C.8 Model selection for diversity of families of arthropods collected on the Seward Peninsula, AK, during summers 2015 and 2016. Final model shown in bold.

Sample Type	Predictor(s)	Year incl.?	AIC	AICc	k	log-likelihood
Pitfall	**EricaceousCover + EricaceousCover^2 + BirchHeight + BirchHeight^2 + TallWillowCover + East**	**N**	**-12.2**	**-11.8**	**10**	**16.11**
	BirchHeight + BirchHeight^2 + TallWillowCover	N	-11.6	-11.3	7	12.78
	EricaceousCover + EricaceousCover^2 + BirchHeight + BirchHeight^2 + TallWillowCover	N	-11.1	-10.7	9	14.50
	EricaceousCover + EricaceousCover^2 + BirchHeight + BirchHeight^2 + TallWillowCover + TallWillowCover^2 + East	N	-10.7	-10.3	11	16.30
	EricaceousCover + BirchHeight + BirchHeight^2 + TallWillowCover	N	-10.7	-10.4	8	13.30
	EricaceousCover + EricaceousCover^2 + BirchHeight + BirchHeight^2 + TallWillowCover + TallWillowCover^2 + East + Slope	N	-8.8	-8.4	12	16.40
	EricaceousCover + EricaceousCover^2 + BirchHeight + BirchHeight^2 + TallWillowCover + TallWillowCover^2 + North + East + Slope	N	-6.8	-6.3	13	16.40
	Null Model	N	-1.8	-1.6	4	4.89
Sweep	**EricaceousCover + BirchCover + BirchCover^2 + North**	**N**	**-8.0**	**-7.7**	**8**	**11.98**
	EricaceousCover + BirchCover + BirchCover^2	N	-7.2	-6.9	7	10.59
	EricaceousCover + BirchCover + BirchCover^2 + North + Slope	N	-6.6	-6.3	9	12.30
	EricaceousCover + BirchCover + BirchCover^2 + North + East + Slope	N	-4.7	-4.3	10	12.26
	EricaceousCover + BirchCover + BirchCover^2 + TallWillowCover + North + East + Slope	N	-2.8	-2.3	11	12.28
	EricaceousCover + BirchCover + BirchCover^2 + TallWillowCover + TallWillowCover^2 + North + East + Slope	N	-0.9	-0.4	12	12.42
	EricaceousCover + EricaceousCover^2 + BirchCover + BirchCover^2 + TallWillowCover + TallWillowCover^2 + North + East + Slope	N	1.1	1.6	13	12.47
	Null Model	N	4.0	4.2	4	1.98

Table 2-C.9 Coefficients and statistical significance of parameters included in final models of arthropod richness (Table 2-C.6), evenness (Table 2-C.7), and diversity (Table 2-C.8).

Sample Type	Response	Parameter	Estimate	*P*-value
Pitfall	Richness	Willow Cover	0.0110	<0.001
		Ericaceous Cover	0.1136	0.029
		Ericaceous Cover^2	-0.0010	0.093
		Birch Height	0.0938	0.469
		Birch Height^2	-0.0105	0.092
		E aspect	1.0375	0.031
	Evenness	Birch Height	0.0069	0.026
		Birch Height^2	-0.0004	0.013
		N aspect	-0.0176	0.100
	Diversity	Willow Cover	0.0049	0.001
		Ericaceous Height	0.0343	0.163
		Ericaceous Height^2	-0.0026	0.066
		Birch Height	0.0339	0.004
		Birch Height^2	-0.0018	0.001
		E aspect	0.0662	0.076
Sweep	Richness	Willow Height	0.1239	0.003
		Willow Height^2	-0.0006	0.026
		Birch Height	0.2819	0.048
		Birch Height^2	-0.0101	0.139
	Evenness	Willow Cover	-0.0013	0.025
		Birch Cover	0.0031	0.074
		Ericaceous Cover	-0.0013	0.038
	Diversity	Ericaceous Cover	-0.0072	<0.001
		Birch Cover	0.0506	<0.001
		Birch Cover^2	-0.0023	0.002
		N aspect	-0.0690	0.096

CHAPTER 3. HIGH DIET DIVERSITY OF ARCTIC PASSERINE NESTLINGS REVEALED BY NEXT-GENERATION SEQUENCING[1]

3.1 ABSTRACT

Arctic passerines occupy an environment that is rapidly being altered due to climatic changes. Recent increases in shrub cover have changed available nesting habitat and the abundance of prey. Earlier, warmer springs drive advances in the emergence of insect prey. However, we still know little about how Arctic passerines may respond to changes in prey availability and their role in Arctic food webs. We characterized nestling diet using next-generation sequencing of fecal matter from 5 common passerines that occupy a gradient of Arctic habitats from open tundra to shrub thicket: Lapland Longspur (*Calcarius lapponicus*), Savannah Sparrow (*Passerculus sandwichensis*), American Tree Sparrow (*Spizelloides arborea*), Golden-crowned Sparrow (*Zonotrichia atricapilla*), and Gray-cheeked Thrush (*Catharus minimus*). Concurrently, we collected arthropods weekly via sweep-net and pitfall traps as measures of prey availability. We found that nestlings were fed prey from all trophic levels, with 7–12 different prey taxa per fecal sac. Common prey, found in >50% of all fecal samples, were dance flies (Empididae), geometrid caterpillars (Geometridae), and sawfly larvae (Tenthredinidae). Diets of Arctic nestlings were equally diverse as or more diverse than those of temperate passerine nestlings analyzed with similar methods. Diet composition varied significantly among species, although the amount of variance explained by species identity was low (nonparametric multivariate analysis of variance, $R^2 = 0.13$), indicating high variation within species. Within species, location explained more variance ($R^2 = 0.21$) in diet composition than

[1] McDermott, M. T., C. M. Handel, P. Doak, and G. A. Breed. High diet diversity of arctic passerine nestlings revealed by next-generation sequencing. In preparation for submission to the Auk.

year, day of season, or nestling age, suggesting responsiveness to local availability. We predict that high diet diversity and the ability to adjust diet composition in response to local availability may protect these birds against negative impacts from future shifts in prey phenology, and that continued increases in shrub cover may drive increases in prey availability for nestlings.

3.2 INTRODUCTION

Insectivorous passerines in the Arctic occupy a rapidly changing environment. Breeding songbirds rely heavily on arthropod prey, which are generally sensitive to both temperature and precipitation (Bale et al. 2002, Sangle et al. 2015). Thus, directional changes or increased variability in climatic factors could significantly affect songbird reproduction or survival by influencing food availability. For example, in many northern areas the phenology of arthropod prey is advancing due to earlier, warmer springs, leading to potential trophic mismatches for some birds that are less plastic in their phenological responses. Evidence for mismatch has been found in shorebirds (Tulp and Schekkerman 2008, McKinnon et al. 2012) and some temperate passerines, particularly those that specialize on a few prey items, migrate long distances, and occupy highly seasonal habitats (Both et al. 2010, Visser et al. 2012), but this phenomenon has been little studied in Arctic passerines. In addition to temperature, summer precipitation and extreme winds are projected to increase in Arctic Alaska (SNAP 2017), which may cause increased variation in daily food availability (Bolduc et al. 2013). However, not all climate-driven changes will likely be detrimental to songbirds. Across the Arctic, woody shrubs are expanding onto open tundra (Racine et al. 2004, Tape et al. 2006), and recent research in Alaska suggests that shrub patches may increase food availability for at least some Arctic passerines (Boelman et al. 2015).

To evaluate the vulnerability of different songbird species to potential climate-related changes in abundance of arthropod prey, it is important to understand diet breadth and prey selectivity not only for adult birds but also in what they feed their young. Many generalist insectivorous songbirds, despite having a diverse diet, show evidence of prey preference (Maher 1979, Holmes and Schultz 1988, Raley and Anderson 1990, Yard et al. 2004). This is particularly true for parents provisioning nestlings, with caterpillars (larval Lepidoptera) being more common in nestling diets than in adult diets for many songbird species (e.g. Maher 1979, Biermann and Sealy 1982, Moreno 1987, Holmes and Schultz 1988). Diet composition can influence nestling condition in some passerines (Garcia-Navas and Sanz 2011, Burger et al. 2012), but some songbirds have been shown to adjust their diet composition to reflect local availability when preferred prey are not available (Busby and Sealy 1979, Grundel and Dahlsten 1991). For example, in a study of the Red-eyed Vireo (*Vireo olivaceus*), experimentally removing preferred prey (caterpillars) did not affect reproductive outcomes (Marshall et al. 2002). Because there is such variation among passerines, it is hard to predict how Arctic species may respond.

Understanding the diversity of nestling diets of Arctic passerines will provide key information on how the population dynamics of these species may be influenced by changes in the abundance and phenology of arthropod prey (Tulp and Schekkerman 2008). To assess potential risks and rewards of climate-driven changes in prey availability for migratory songbirds, we need detailed information on diet composition. Songbird diet in the Arctic is particularly understudied, except for the Lapland Longspur (Custer and Pitelka 1978, Seastedt 1980). Without diet information specific to each passerine species, it remains difficult to assess how climate-induced changes in vegetation and food availability will affect migratory songbirds.

Our current understanding of avian nestling diets stems largely from morphological identification of prey photographed with nest cameras or collected via emetics, ligatures, fecal sacs, or stomach contents. These techniques, however, are biased against detection of small, soft-bodied prey and can be invasive (Pompanon et al. 2012). In addition, attaining species-level identification can be impossible with fragments of arthropods found in stomachs or fecal matter, and difficult even with intact specimens. Next-generation sequencing (NGS) of fecal matter is a relatively new, non-invasive technique that can reveal trophic relationships that are difficult to resolve using morphological techniques (Kress et al. 2015). NGS allows species-level identification of a greater diversity of prey items than traditional methods, although degradation of DNA during digestion prevents lower-level classification of all sequences (Kress et al. 2015). NGS of fecal samples has been used primarily in mammalian systems (e.g. Bowles et al. 2011, Hamad et al. 2014), especially bats (e.g. Bohmann et al. 2011, Razgour et al. 2011, Zeale et al. 2011, Vesterinen et al. 2013), but applications in avian systems are growing (Jedlicka et al. 2013, King et al. 2015, Crisol-Martinez et al. 2016, Jedlicka et al. 2017).

Despite recent advances in NGS, there are still limitations to the information this technique can provide. Many primers used in PCR for arthropod DNA preferentially amplify sequences from a few orders (Pompanon et al. 2012, Clarke et al. 2014), limiting the usefulness of NGS as a quantitative measure of prey use. Recent studies have developed methodology to improve quantitative estimates and reduce taxonomic bias (Saitoh et al. 2016, Thomas et al. 2016), but, generally, the number of DNA sequence reads is not a reliable quantitative measure of diet composition due to primer and digestion bias (Elbrecht and Leese 2015, Pinol et al. 2015, Jedlicka et al. 2017). In addition, DNA analysis provides only partial information about ecological interactions because it cannot identify the life stage or sex of prey, which may differ

in size, caloric value, habitat preference, and/or trophic level. These attributes will influence spatial and temporal availability of prey to the foraging adults and their importance as food items to the nestlings.

Identifying key prey items and their ecological functions will also help us to understand community dynamics and the role of passerines in Arctic food webs. Although the present study is focused on food availability and use, we also examine the trophic levels of arthropod prey used by nestlings to inform future research on trophic cascades between songbirds, arthropods, and plants. Research using NGS in agricultural systems has revealed that nestlings eat mostly herbivorous insects, thereby benefiting plants (Crisol-Martinez et al. 2016, Jedlicka et al. 2017). If Arctic songbird nestlings provide a similar ecological function, songbird density could function as a positive feedback of shrub expansion.

In this study we used NGS to characterize nestling diet of 5 common insectivorous migratory passerines: Lapland Longspur (*Calcarius lapponicus*), American Tree Sparrow (*Spizelloides arborea*), Golden-crowned Sparrow (*Zonotrichia atricapilla*), Savannah Sparrow (*Passerculus sandwichensis*), and Gray-cheeked Thrush (*Catharus minimus*). These birds nest in a variety of Arctic habitats from graminoid tundra to shrub thickets (Table 3.1), often in close proximity to each other because of heterogeneous habitat mosaics. Because all are ground-feeders, they may use overlapping foraging habitats. All 5 species are thought to feed their young insects almost exclusively, although there is a pronounced lack of data on nestling diet for the American Tree Sparrow, Golden-crowned Sparrow, and Gray-cheeked Thrush (Norment et al. 1998, Lowther et al. 2001, Naugler et al. 2017). We chose to study nestlings because their exclusively insectivorous diet may make them more responsive to changes in availability of arthropod prey, which could thus be a strong driver of songbird population dynamics. In

Table 3.1 Natural history of focal arctic passerine species using a tundra–shrub habitat gradient on the Seward Peninsula, Alaska, USA.

Species	Foraging	Nest Placement	Habitat	Breeding Distribution
Lapland Longspur[1]	Ground	Ground	Graminoid tundra	Alaska, N. Canada, Greenland
American Tree Sparrow[2]	Ground	Ground, base of shrubs	Mixed tundra and low–medium shrub	Alaska, N. Canada
Golden-crowned Sparrow[3]	Ground	Ground, base of shrubs	Mixed tundra and low–medium shrub	Alaska, W. Canada
Savannah Sparrow[4]	Ground	Ground	Graminoid tundra and low shrubs	Alaska, Canada, N. & W. USA
Gray-cheeked Thrush[5]	Ground	Shrubs	Medium–tall shrub thickets	Alaska, N. Canada

[1]Hussell and Montgomerie (2002)
[2]Naugler et al. (2017)
[3]Norment et al. (1998)
[4]Wheelwright and Rising (2008)
[5]Lowther et al. (2001)

addition, nestlings are easy to sample and are restricted to one location for a period of time, allowing us to assess prey available to foraging parents within the immediate area.

To understand how prey availability may influence provisioning patterns, we quantified the relative strength of spatial, temporal (Julian day, year), and biological (bird species, nestling age) factors in explaining variation in diet composition. We used Golden-crowned Sparrows as a case study to test if selection of particular prey was related to availability. To evaluate traits that could influence birds' ability to cope with a changing food supply, we tested for differences among species in diet diversity and quantified the relative strength of spatial and temporal variables on diet composition. We identified common prey items potentially important to future research on reproductive outcomes and nestling growth. To understand the trophic interactions of songbird nestlings and arthropods, we categorized the prey frequently used by each species by guild.

3.3 METHODS

3.3.1 Study Area

We established 2 study sites, one interior (64.93°N, 164.92°W, elevation 160 m) and one coastal (64.66°N, 164.33°W, elevation 100 m), on the Seward Peninsula of Alaska, USA (Chapter 2, Figure 2.1). The peninsula encompasses a transition zone between boreal forest of interior Alaska and coastal Arctic tundra, across which vegetation is undergoing rapid climate-driven change (Racine et al. 2004, Tape et al. 2006). At each study site, we set up 3 pairs of 600-m × 600- m study plots for nest searching and arthropod sampling during summer in 2015 and 2016. One pair of interior plots was dropped in 2016 due to low bird abundance and logistical constraints and a new plot was established as a replacement. Plots varied in the composition, coverage, and height of shrub vegetation. Shrub thickets of dwarf birch (*Betula nana*), willow (*Salix* spp.), and, less commonly, alder (*Alnus* spp.) occurred in riparian areas and on hillsides, ranging in height from 0.4–2.5 m. Tundra-dominated areas were characterized by graminoid vegetation, forbs, and various species of prostrate or dwarf shrubs <0.4 m tall.

3.3.2 Dietary Sampling

We searched and monitored plots every 2 days during the breeding season (late May to early July) for passerine nests, focusing on our 5 focal species. We collected fecal samples opportunistically when we measured the growth of nestlings at 0–1, 2–3, and 6–7 days of age. We did not measure older nestlings so as to preclude premature fledging, and measured birds ~5 m away from the nest site to minimize disturbance. When measuring, we temporarily placed all nestlings from the nest in a plastic container; we collected all fecal samples from the container with tweezers into a plastic Whirl-Pak (Nasco) sterile sample bag with 100% ethanol (enough to

submerge sample completely); thus, some samples included multiple samples from a brood. Nestlings of our study species typically fledge at 8–11 days (Norment et al. 1998, Hussell and Montgomerie 2002, Wheelwright and Rising 2008, Naugler et al. 2017), except those of Gray-cheeked Thrush, which fledge at 10–13 days (Kessel 1989, Lowther et al. 2001); thus, our sampling represents the majority of the nestling period. We used opportunistic observations of provisioning behavior (11 adult birds observed for 2–15 minutes each) and examination of stomach contents of nestlings (3 Gray-cheeked Thrush nestlings, 3 Lapland Longspur nestlings) found dead to inform our interpretation of NGS sequencing results (see below for details on sequencing). These observations helped clarify whether nestlings were being fed larvae or adults of a given prey taxon.

3.3.3 Arthropod Sampling

We collected arthropods in both pitfall traps and sweep nets at fixed systematic sampling locations once a week for 8 weeks (late-May–late-July) each summer. We analyzed a subset of arthropod samples collected concurrently with fecal samples (June 8–July 14, 2015, June 11–July 5, 2016). All focal species (Lapland Longspur, Savannah Sparrow, Golden-crowned Sparrow, American Tree Sparrow, and Gray-cheeked Thrush) are reported to be primarily ground feeders both specifically on the Seward Peninsula (Kessel 1989) and generally across their breeding ranges (Norment et al. 1998, Lowther et al. 2001, Hussell and Montgomerie 2002, Wheelwright and Rising 2008, Naugler et al. 2017). However, these species, especially the American Tree Sparrow, have also been observed preying on flying insects and larvae on low vegetation in our study area (Kessel 1989). Therefore, we focused our collection methods on arthropods within the

foraging range of ground feeders and gleaners. Sweep netting targets flying insects and larvae on vegetation, and pitfall trapping targets ground-dwelling arthropods such as beetles and spiders.

We placed 3 pitfall arrays 200 m apart along a transect down the center of each plot. Pitfall arrays consisted of 3 cups 7.6 cm in diameter and 16.5 cm tall placed 1 m apart, buried to the rim, and filled with propylene glycol to a depth of 2 cm. On each collection date, we combined all 3 cups from an array into a single sample for identification and analysis. In a few cases when pitfalls had been open for 6 or 8 days instead of 7, the counts of arthropods caught were adjusted by multiplying them by a correction factor so that all pitfall abundance estimates were normalized to an equivalent of 7 days. Each sweep-net transect consisted of 50 side-to-side sweeps beginning at a pitfall array and extending 25 m in a random direction on each sampling date. The net was aimed to sweep the top 25% of vegetation within a 2 m swath along the transect line. Sweep nets were heavy-duty cotton muslin bags, 38 cm in diameter, on a sturdy 0.9-m wooden handle. We conducted 2 (in 2015) or 3 (in 2016) sweep-net transects per plot each week for a total of 8 weekly sweep-net sampling periods each year. Where appropriate, we used the average of all samples caught on a plot to control for variation in sampling between years.

Sweep-net and pitfall samples were sorted and all individuals were identified to family for most groups using published keys (Triplehorn and Johnson 2005, Marshall 2006). Some groups could only be identified to order (Lepidoptera, Araneae) and some to superfamily (Aphidoidea, Schizophora) due to the difficulty of distinguishing families of these groups and a lack of published keys for Arctic taxa. Individuals within each taxon were counted separately by life stage (larvae, nymph, adult). We dried >30 individuals of each family of arthropods for 48 hr at 40 °C and used mean dry mass to estimate total biomass per sample based on counts of individuals. For rare taxa with fewer than 30 specimens we measured as many individuals as

possible. See Table 2-A.2 in Appendix 2-A for biomass data and sample sizes. For taxa that varied in size, we separated a subsample of individuals into several size classes by length and measured their biomass. We then estimated total biomass for that taxon by multiplying total counts of arthropods within each size class by mean biomass of that size class.

We assigned arthropods to trophic guild (herbivore, predator, decomposer, parasite, parasitoid, non-feeding, or other) based on reference to standard entomology texts (Triplehorn and Johnson 2005, Marshall 2006) and online taxonomy databases (Maddison et al. 2007, Parr et al. 2014).

3.3.4 DNA Sequencing Protocol

We submitted 145 fecal samples to Jonah Ventures LLC (Manhattan, KS) for sequencing. Arthropod-specific primers (ZBJ primers developed in Zeale et al. 2011) were used to target the CO1 gene for amplification, and sequencing was performed with an Illumina MiSeq (Illumina, San Diego, California, USA). Sequence identity was assigned with the Barcode of Life Database (BOLD) using QIIME, and sequences without identification to the family level or below were discarded. We chose to use BOLD due to a recent effort to barcode and archive sequences of Alaskan invertebrates in that database (Sikes et al. 2016). Any taxa without genus- or species-level matches were grouped by the next highest taxonomic classification assigned, so that estimates of total species and genera were conservative. All non-arthropod sequence results (e.g., passerine, lichen, rotifer, or plant DNA) were ignored in dietary analysis. The amount of DNA (number of reads) recovered and amplified from each sample ranged from 1–57,791 (median 6,248). Twenty-four samples that amplified poorly (<500 sequence reads) (J. Craine, personal communication) were not included in further analysis. To control for the increased diversity and

detectability of prey in fecal samples in which prey DNA amplified well, molecular operational taxonomic unit (MOTU) tables were rarefied to even sequencing depth (598 reads, the minimum recovered from a sample that passed quality filtering). See Appendix 3-A for details on DNA extraction, amplification, and sequencing as well as further details on bioinformatic processing.

To assess bias due to amplification and differential digestion, we prepared 2 replicate samples of a mixture of arthropods from 13 orders and 29 families that had been collected on our study sites, preserved in 100% ethanol, freeze-dried, weighed by taxon, and then pulverized into a homogenous mixture. The two replicate samples of known mixed dry biomass were then processed simultaneously with nestling fecal samples. Comparisons of DNA recovery and biomass of the known mixed samples indicated significant taxonomic bias (Figure 3-B.1 in Appendix 3-B); thus, we use only presence-absence metrics in our analyses of nestling diet based on fecal samples.

3.3.5 Statistical Analysis

We summarized diet composition for each bird species by prey taxon and trophic guild by calculating the frequency of occurrence of arthropods detected in the fecal samples. We then conducted a nonparametric multivariate analysis of variance to test the effect of bird species on diet composition, and within species, the effect of spatial factors (study site and plot nested within site), temporal factors (day within season, year), and biological factors (bird species, nestling age) on diet composition using the function 'adonis' in package 'vegan' (v. 2.4-2; Oksanen et al. 2015) in the R statistical framework (v. 3.3.3; R Core Team 2015). Analysis of variance using distance matrices (ADONIS) uses a dissimilarity matrix (Bray-Curtis distances between compositions of fecal samples) to partition variation and calculates the significance of

associated variables with permutation tests. Because ADONIS can be sensitive to heterogeneity in grouping factors (Anderson and Walsh 2013), we tested explanatory variables for homogeneity of multivariate dispersion before conducting the analysis.

To examine the response of each bird species to prey availability, we first qualitatively compared prey selection (frequency of occurrence of a given arthropod order in fecal samples) to relative prey availability as measured by total biomass of each order of arthropods collected in 2015 and 2016 across all sites during the 8-week periods when fecal samples were collected. To identify arthropods used more or less than expected based on total availability, for each bird species we standardized frequency of consumption and available biomass (log-transformed) across 10 orders of arthropods. Mean consumption was defined as the mean frequency of occurrence of 10 arthropod orders in nestling fecal matter. Mean biomass was calculated by averaging the total biomass caught of all 10 orders. We plotted use vs. availability (evaluated separately for pitfall and sweep net samples) and we interpreted mean values above or below the 1:1 identity line as selection or avoidance, respectively, of a given prey taxon. We conducted a more rigorous quantitative analysis of the relationship between consumption and availability for the Golden-crowned Sparrow, which had the largest number of fecal samples. For this species, we examined whether the occurrence of prey most frequently detected in fecal matter was significantly related to local availability. Specifically, we conducted separate logistic regressions (R package 'lme4'; (Bates et al. 2015) for each of the 3 most common prey items to test whether their presence or absence in the feces of a nestling was related to the prey's biomass in sweep-net samples on the nestling's plot during the closest sampling period (generally within 3 days of when the fecal sample was collected).

High dietary diversity, measured at the population level, can result from either all individuals within the population feeding on a wide variety of foods or a collection of individuals each with relatively restricted diets and little overlap among individuals. To compare individual diet diversity among species, we tested for differences in mean richness (number of taxa) per fecal sample using a non-parametric analysis of variance (Kruskal-Wallis test) and performed post-hoc pairwise comparisons between bird species (function 'kruscalmc' in R package 'pgirmess' v. 1.6.7; (Giraudoux 2017). To compare overall diet diversity among the 5 species, we built rarefaction curves with 95% confidence intervals (Gotelli and Colwell 2001).

3.4 RESULTS

3.4.1 Diet Composition

We submitted 145 fecal samples from 125 nests of 6 bird species for molecular sequencing. Among these, 117 yielded usable sequence data (Table 3-C.1 in Appendix 3-C). Although each sample represented 1 collection at 1 nest, some samples contained multiple fecal sacs and some nests were resampled on different dates. To control for this variation and avoid pseudoreplication, we restricted our statistical analysis to a subset of the samples that had only 1 fecal sac per nest (representing 60 unique nests from 5 species; Table 3.2). Sequencing of the subset revealed arthropods belonging to 11 orders, 56 families, and 86 species (Table 3-C.2 in Appendix 3-C). Including sequences that were identified only to genus or family, we found 163 unique classifications (MOTUs). Although several arthropod families occurred frequently in the

Table 3.2 Number of fecal samples analyzed from nestlings of 5 passerine species in northwestern Alaska in 2015 and 2016.

Species	2015	2016	Total
American Tree Sparrow	2	6	8
Golden-crowned Sparrow	8	10	18
Gray-cheeked Thrush	4	8	12
Lapland Longspur	9	8	17
Savannah Sparrow	5	0	5

nestling diets of all 5 passerines, occurrence of other families was highly variable among species, and nestlings of all species were fed prey from multiple trophic levels (Table 3.3).

Table 3.3 Arthropod families detected in 60 fecal samples from nestlings of 5 passerines in northwestern Alaska in 2015 and 2016. Values represent frequency of occurrence (% of samples) in nestling diet for each species. Guild designations are based on the life stage most likely in the diet. For example, Tenthredinidae are listed as herbivores although adults are predaceous because stomach samples and field observations revealed only larval stages in diets. Families designated "other" are omnivorous or contain species from multiple guilds.

Order	Family	Guild	American Tree Sparrow *n = 8*	Golden-crowned Sparrow *n = 18*	Gray-cheeked Thrush *n = 12*	Lapland Longspur *n = 17*	Savannah Sparrow *n = 5*
Araneae	Araneidae	predator	-	6	-	6	20
	Clubionidae	predator	-	-	-	6	-
	Linyphiidae	predator	12	11	25	18	20
	Lycosidae	predator	-	11	-	18	20
	Philodromidae	predator	-	11	-	41	-
Coleoptera	Cantharidae	predator	38	6	8	29	20
	Carabidae	predator	-	6	17	24	-
	Chrysomelidae	herbivore	-	6	-	-	-
	Curculionidae	herbivore	-	-	8	-	-
	Leiodidae	decomposer	-	-	-	6	-
	Staphylinidae	predator*	-	-	-	12	-
Diptera	Anthomyiidae	herbivore	12	-	-	18	20
	Calliphoridae	decomposer	-	-	-	-	20
	Ceratopogonidae	parasite*	-	11	-	-	-
	Chironomidae	non-feeding*	25	11	17	6	40
	Culicidae	other*	25	22	-	6	40
	Cylindrotomidae	non-feeding	-	17	-	-	-
	Dolichopodidae	predator	-	6	-	6	-
	Empididae	predator	62	83	42	88	100
	Hybotidae	predator	12	-	-	-	-
	Keroplatidae	predator	-	6	-	-	-
	Limoniidae	non-feeding	-	-	8	6	-
	Muscidae	other*	25	6	-	18	-
	Mycetophilidae	decomposer	25	6	-	-	-
	Rhagionidae	predator	25	6	-	6	-
	Scathophagidae	predator	-	-	-	6	-
	Syrphidae	other*	50	28	8	29	40
	Tachinidae	parasite	-	11	-	-	-

Table 3.3, cont.

Order	Family	Guild	American Tree Sparrow *n = 8*	Golden-crowned Sparrow *n = 18*	Gray-cheeked Thrush *n = 12*	Lapland Longspur *n = 17*	Savannah Sparrow *n = 5*
	Tipulidae	non-feeding	25	11	58	24	20
Hemiptera	Anthocoridae	predator	-	-	8	-	-
	Aphididae	herbivore	12	-	-	-	-
	Cicadellidae	herbivore	25	6	-	24	-
	Miridae	herbivore	-	11	-	6	-
	Psyllidae	herbivore	38	17	17	6	20
Hymenoptera	Braconidae	parasitoid	-	-	8	-	-
	Cimbicidae	herbivore	12	6	-	-	-
	Encyrtidae	parasitoid	-	6	-	-	-
	Ichneumonidae	parasitoid	-	6	17	6	-
	Platygastridae	parasitoid	-	-	-	6	-
	Proctotrupidae	parasitoid	-	-	-	6	-
	Tenthredinidae	herbivore	62	33	75	65	60
Lepidoptera	Depressariidae	herbivore	-	-	-	18	-
	Elachistidae	herbivore	-	-	-	6	-
	Erebidae	herbivore	-	-	-	6	-
	Geometridae	herbivore	88	50	67	65	80
	Lycaenidae	herbivore	-	-	-	6	-
	Noctuidae	herbivore	-	22	8	29	60
	Nymphalidae	herbivore	-	6	-	18	-
	Papilionidae	herbivore	-	6	-	-	-
	Tortricidae	herbivore	12	17	8	41	20
	Ypsolophidae	herbivore	12	-	-	-	-
Neuroptera	Hemerobiidae	predator	-	-	8	6	-
Plecoptera	Chloroperlidae	non-feeding	-	-	8	-	-
Symphypleona	Sminthuridae	decomposer	-	-	-	-	20
Trichoptera	Limnephilidae	non-feeding	25	6	8	-	-

*Members of this family may also serve as pollinators.

The diet items most frequently encountered among individual nestlings of all species were predaceous dance flies (Empididae, found in 72% of all fecal samples), herbivorous geometrid caterpillars (Geometridae, 63% of all fecal samples), and herbivorous sawfly larvae (Tenthredinidae, 55% of all fecal samples). Seven parasitoid taxa that use caterpillars, sawfly larvae, and leafhoppers (Cicadellidae) as hosts were detected in 5 fecal sacs, often with host

DNA. However, in two instances parasitoids were detected in fecal samples with no host DNA, suggesting direct consumption of adult parasitoid individuals.

While there were striking similarities among the 5 focal species in the prey taxa most frequently fed to nestlings, there was also significant interspecific variation in diet composition ($R^2 = 0.13$, $P < 0.001$; Figure 3.1A). Gray-cheeked Thrush nestlings were fed hoverflies (Syrphidae) less often and crane flies (Tipulidae) more often than were nestlings of other species. Longspurs were fed crab spiders (Philodromidae) more frequently than were the other species. Savannah Sparrows were fed mosquitoes (Culicidae) and chironomid midges (Chironomidae), both of which are swarming flies with aquatic larval stages, more frequently than were other species (Table 3.3).

3.4.2 Prey Availability and Consumption

The frequency of occurrence of prey fed to nestlings corresponded well to their availability as measured by biomass, particularly in sweep-net samples, with Diptera, Hemiptera, Hymenoptera, and Lepidoptera accounting for a large proportion of the arthropod prey recovered from fecal matter (Figure 3.1A) and biomass in sweep-net samples (Figure 3.1B). These arthropod taxa were also present in, but did not dominate, the biomass of pitfall traps. Hemiptera were found in fecal samples less frequently than Diptera or Hymenoptera, although these 3 orders of insects accounted for similar amounts of biomass recovered in sweep-net samples.

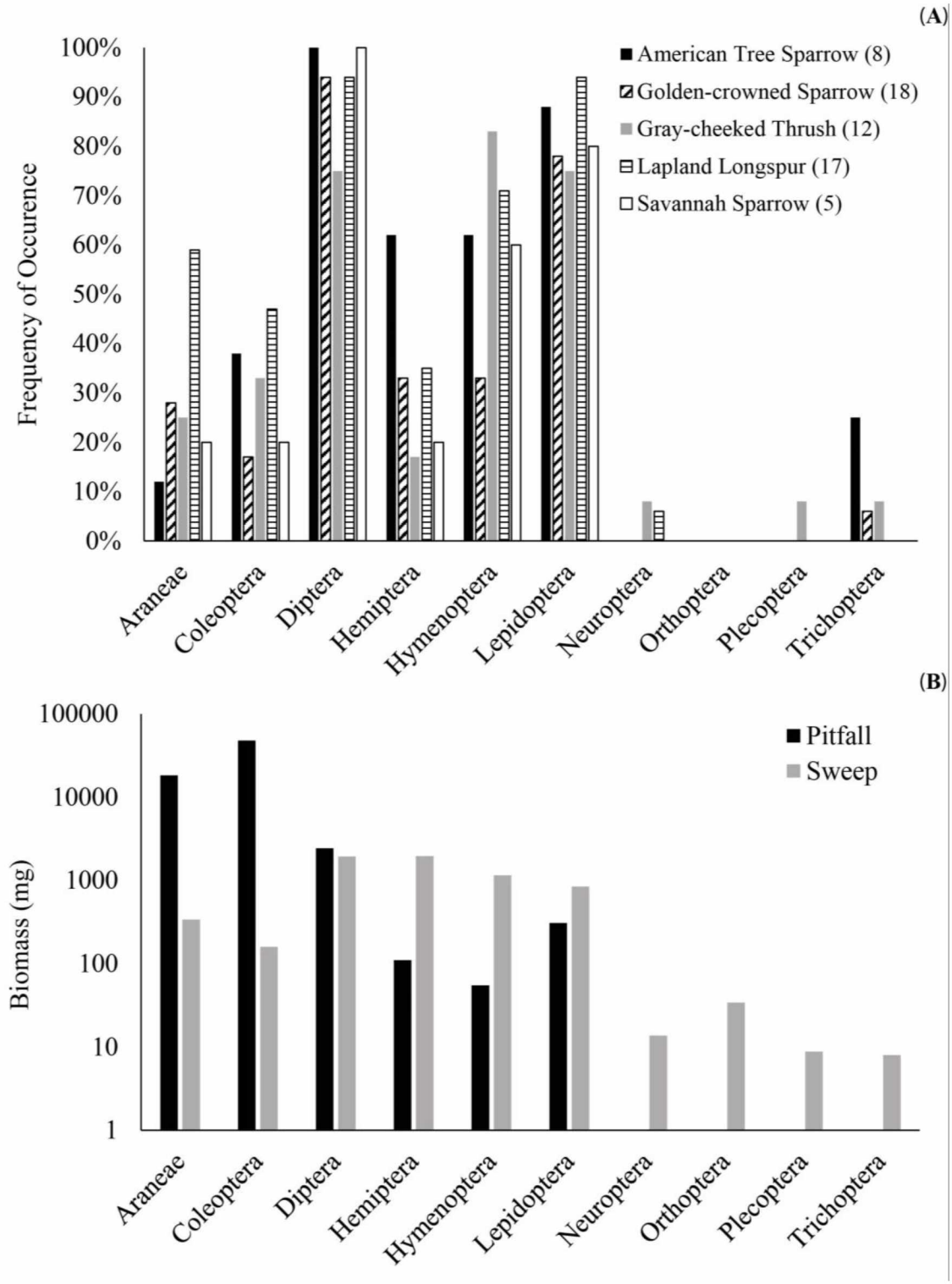

Figure 3.1 Arthropod prey consumption (A) and availability (B). Panel (A) shows the frequency of occurrence of 10 orders of arthropods in nestling diet for 5 passerine species in northwestern Alaska in 2015 and 2016. Panel (B) shows dry biomass of these arthropods in pitfall and sweep-net samples during the 8-week period each season in which fecal samples were collected. Note that biomass is shown on a logarithmic scale.

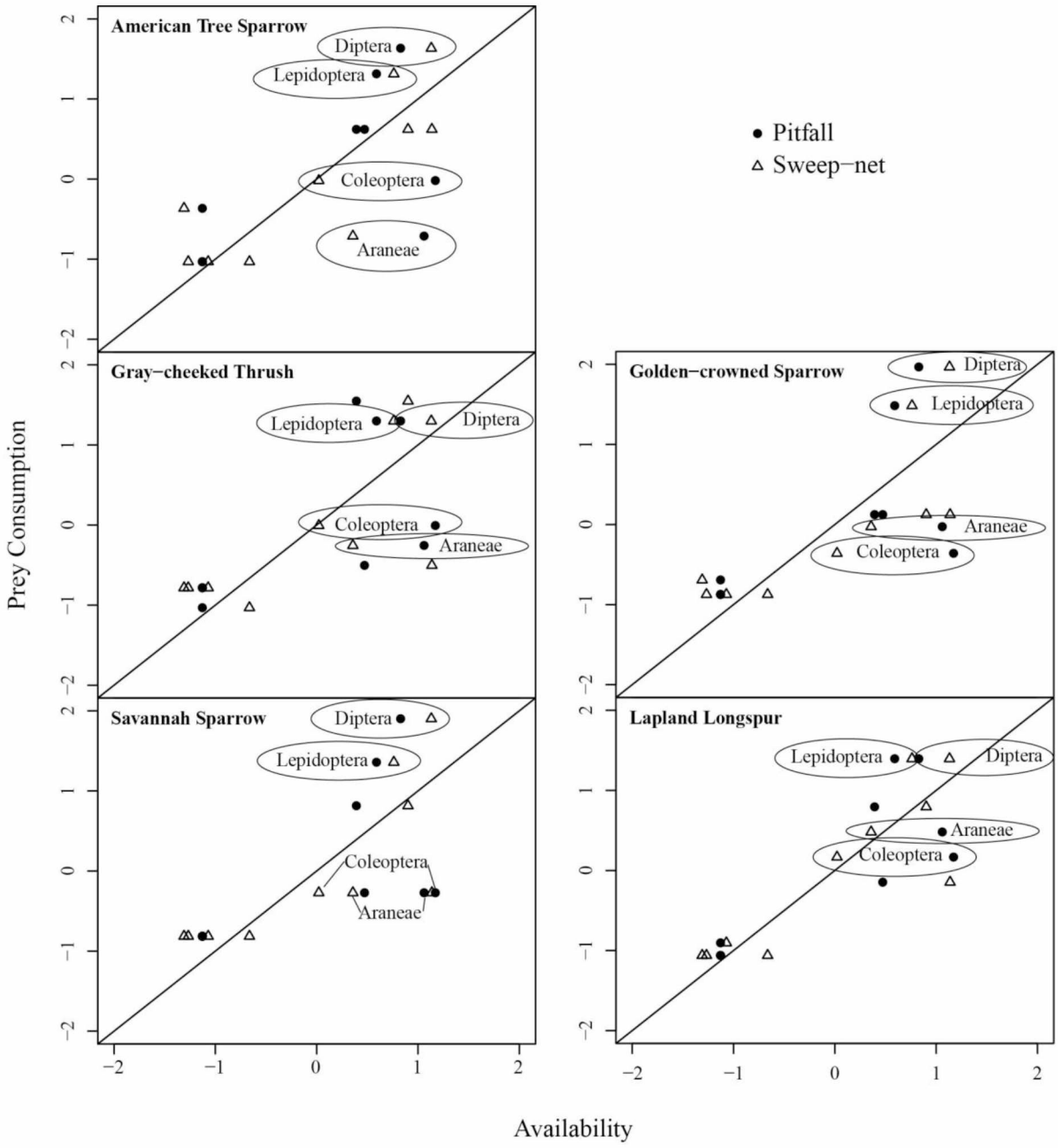

Figure 3.2 Prey consumption (frequency of occurrence in nestling fecal samples) of 10 arthropod orders as a function of dry biomass available as measured in pitfall traps and sweep-net samples. Consumption and availability (log-transformed biomass) were standardized to mean 0 and SD = 1 for each passerine species. Orders above 1:1 identity line were consumed more frequently than expected based on availability, and orders below 1:1 line were consumed less frequently than expected.

Insects in the orders Diptera and Lepidoptera were the most frequently detected prey in fecal samples and both orders were fed to nestlings of all 5 species more often than expected based on comparisons of standardized availability and consumption (Figure 3.2). In contrast, Araneae and Coleoptera were fed to nestlings of all 5 species less often than expected. Araneae DNA was not amplified well by the primers used in fecal analyses and spiders may therefore be more commonly consumed than we detected.

Younger nestlings were fed more Lepidoptera and Tenthredinidae (presumably both in larval stages, based on observations and stomach samples) and fewer hard-bodied flies (Diptera) than were older nestlings. Year ($R^2 = 0.03$, $P = 0.002$) and day of season ($R^2 = 0.06$, $P < 0.001$) also explained a small but significant amount of variation in diet composition (Table 3.4). All three major prey groups (Lepidoptera larvae, Tenthredinidae larvae, and Empididae adults) exhibited interannual and seasonal variation in availability (Figure 3.3). The greatest amount of variation in frequency of prey fed to nestlings was explained by study plot nested within the coastal and interior sites ($R^2 = 0.21$, $P = 0.009$; Table 3.4). Based on multivariate dispersion tests, variances of both plot ($P < 0.001$) and day of season ($P < 0.001$) were heterogeneous among bird species, and this may account for some of the significance of these 2 variables. Heterogeneous variance indicates some bird species were more consistent across plots and days than other species, but since this variation is still of biological interest, these variables were retained in model.

Table 3.4 Results from analysis of variance using distance matrices (ADONIS) showing the amount of variation in nestling diet composition within 5 passerine species explained by biological, spatial, and temporal covariates. Avian species was included as a blocking factor.

Source of variance	R^2	P
Nestling age	0.03	<0.001
Site	0.02	0.29
Year	0.03	0.002
Day of season	0.06	<0.001
Plot	0.21	0.009

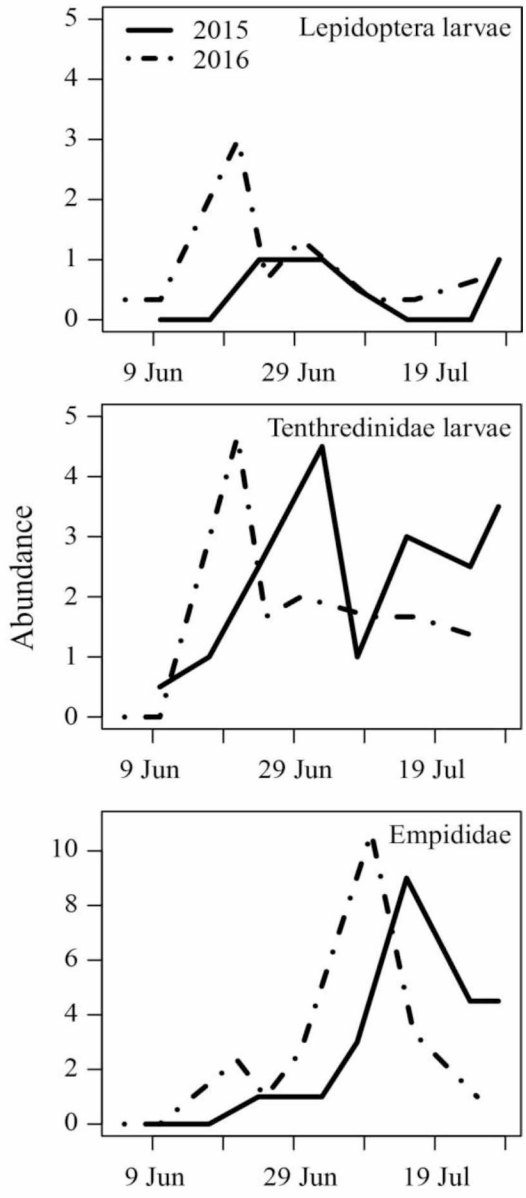

Figure 3.3 Availability of 3 major groups of arthropod prey fed to passerine nestlings over 2 years (2015 vs. 2016), and day of season. Availability is measured by mean number of arthropods in several sweep-net samples collected per plot in northwestern Alaska. For clarity, abundance on a single study plot is shown.

Golden-crowned Sparrow nestlings were most frequently fed prey from 3 groups of arthropods (Table 3.5), all of which varied temporally in availability (Figure 3.3): Empididae, which occurred in 83% of fecal samples, Lepidoptera (presumably larvae, based on observations), which occurred in 78% of fecal samples, and Tenthredinidae (presumably larvae, based on observations), which occurred in 33% of fecal samples. Logistic regression showed that the occurrence of Tenthredinidae DNA in a fecal sac was positively associated with the biomass of Tenthredinidae collected in sweep-net samples on the nestling's plot the same week (pseudo-R^2 = 0.26, P = 0.04; Table 3.5). However, occurrence was not related to sweep-net biomass for either Lepidoptera or Empididae.

Table 3.5 Logistic regression of prey fed to Golden-crowned Sparrow nestlings in northwestern Alaska as a function of prey biomass measured via 3 sweep-net transects on the same 36-ha plot within 6 days of collection of the fecal sample. In all plots available biomass was the predictor.

Response	Estimate	SE	*P*	pseudo-R^2
Lepidoptera in fecal sac (Y/N)	0.02	0.02	0.37	0.05
Empididae in fecal sac (Y/N)	0.08	0.37	0.83	0.00
Tenthredinidae in fecal sac (Y/N)	0.28	0.14	0.04	0.26

3.4.3 Diet Diversity

We detected 1−19 prey taxa (MOTUs) in each fecal sample, with median richness ranging from 7.5 for Golden-crowned Sparrows to 12 for Lapland Longspurs (Figure 3.4). There was a significant difference among species in richness per fecal sample (Kruskal-Wallis $\chi^2 = 10.67$, df = 4, $P = 0.03$), but post-hoc pairwise comparisons were not significant. There were significant differences among the 5 species in overall diet diversity as measured by rarefaction analysis, with American Tree Sparrow, Lapland Longspur, and Savannah Sparrow having greater diet breadth than Gray-cheeked Thrush and Golden-crowned Sparrow (Figure 3.5).

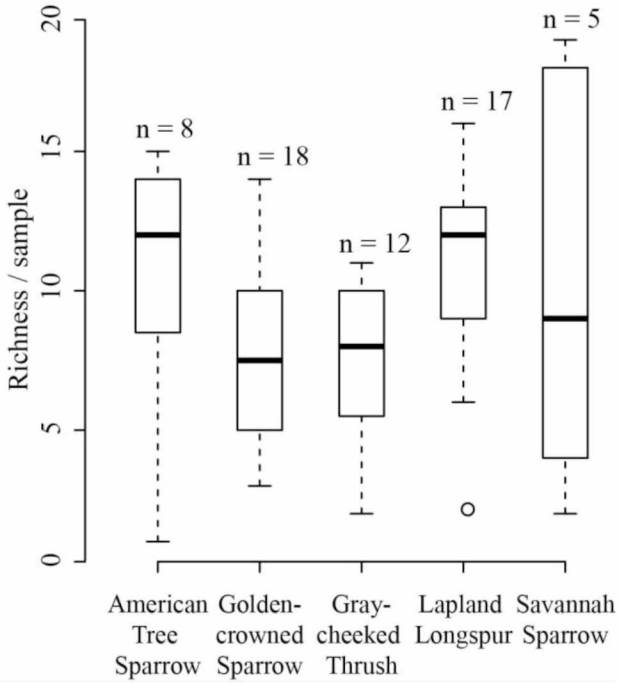

Figure 3.4 Average number of arthropod taxa detected per fecal sample from 5 species of passerine nestlings in northwestern Alaska, USA. Horizontal line represents the median, box encompasses the first and third quartiles, and whiskers show the range of values.

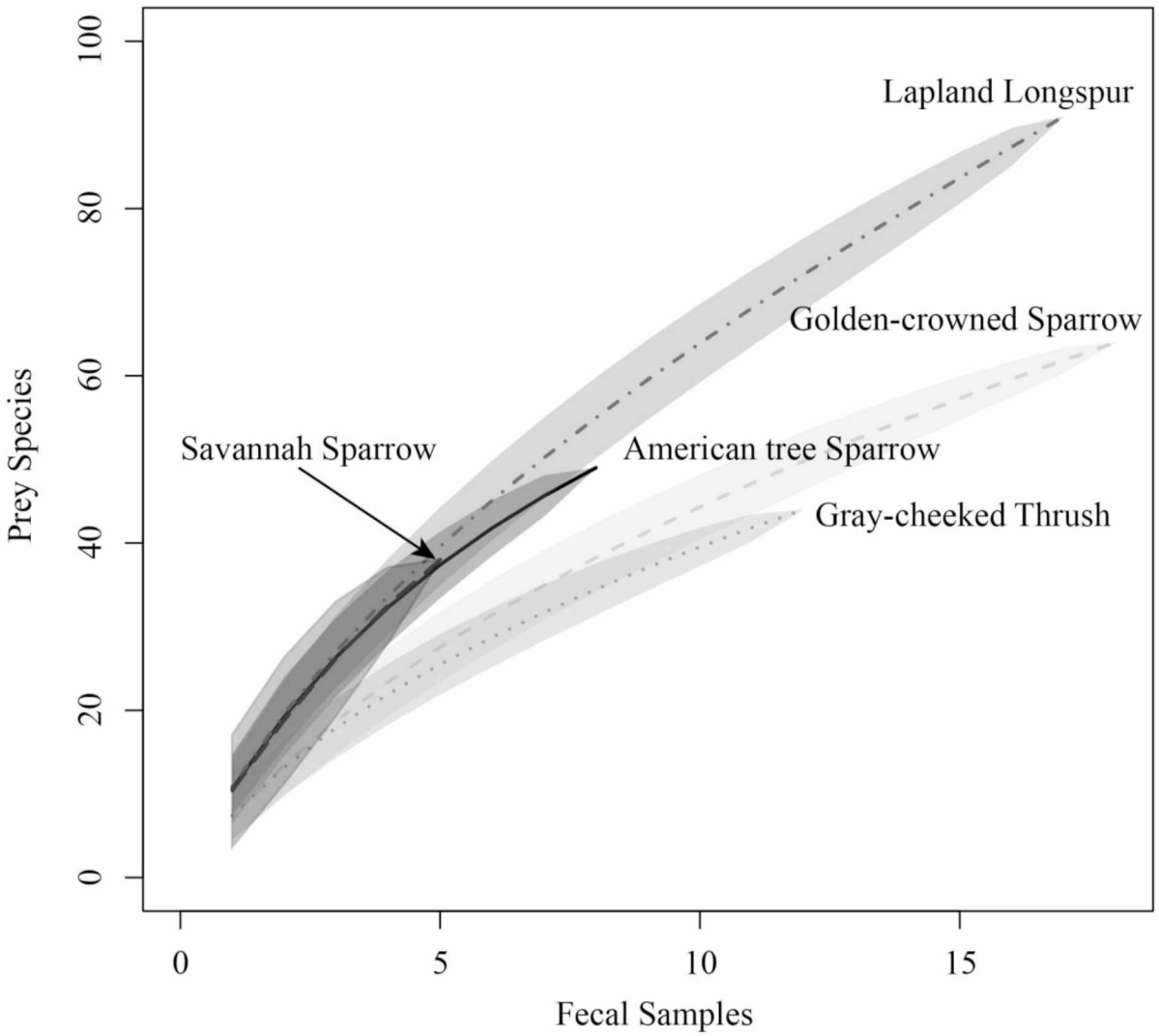

Figure 3.5 Rarefaction analysis of nestling fecal samples from five passerine species. Each line represents the richness (number of prey species) detected in a given number of samples. Envelopes represent 95% confidence intervals. Non-overlap in confidence intervals indicates a significant difference.

3.5 DISCUSSION

We found high diet diversity in nestlings from 5 Arctic passerines, a pattern that may indicate an ability to adjust to phenological changes and increasing fluctuations in prey populations (Colles et al. 2009, Sokolov et al. 2012). Variation in diet within species was primarily influenced by spatial variables, presumably a reflection of local prey availability since

previous analyses showed significant differences among plots in arthropod biomass and community composition (Chapter 2).

Despite the assumption that diet composition changes in response to local prey availability, we did not always find evidence of a relationship. In our case study of Golden-crowned Sparrows, we found that prey availability, as measured by biomass in sweep-net samples, was not a strong predictor of the occurrence of Lepidoptera larvae or Empididae (found in ~80% of fecal samples), although it was a significant predictor for the occurrence of Tenthredinidae larvae (found in a third of fecal samples). High consumption of prey items unrelated to their availability may be evidence of preference (Maher 1979, Raley and Anderson 1990, Yard et al. 2004), and Lepidoptera larvae have been repeatedly documented as a prey source important in passerine nestling diets (Maher 1979, Biermann and Sealy 1982, Moreno 1987, Holmes and Schultz 1988) presumably due to their large size, ease of capture, and high nutritional content (Holmes and Schultz 1988, Razeng and Watson 2015).

There could, however, be alternative explanations for a lack of relationship between sweep-net sampling and nestling diet composition. Sweep-nets may not accurately reflect the prey available to foraging birds, since their ability to attack prey can depend on vegetation structure and environmental conditions (Holmes and Schultz 1988, Poulin and Lefebvre 1997). In addition, sweep-net samples may not have been linked tightly enough (temporally or spatially) to collection of fecal sacs to accurately reflect availability during provisioning trips. Finally, the sensitivity of our analysis of prey selection was relatively low because we could only use NGS to evaluate the presence or absence of prey taxa rather than their abundance or biomass in nestling diet. Combining genetic and morphological approaches to studying diet composition might help to more accurately assess how prey consumption changes with availability.

Differences among species in diet diversity could have implications for their ability to adjust to climate-driven changes in their environments. Generalists are better than specialists at coping with the fluctuations in food supply that are typical of the Arctic (Sokolov et al. 2012), We found that nestlings of all 5 species were provisioned with a wide variety of prey, having an average of 7−12 prey types per fecal sample compared to a range of 2−7 in temperate passerines (Gámez-Virués et al. 2007, Orłowski et al. 2014, Orłowski et al. 2016, Trevelline et al. 2016, Jedlicka et al. 2017). Direct comparison with such studies is complicated, however, by the variety of techniques used to estimate dietary breadth and variation in bioinformatic processing. At the population level, direct comparison becomes even more difficult due to non-linear increases in diversity with sample size (Gotelli and Colwell 2001) and a paucity of research on nestling diet using NGS, which tends to reveal a greater diversity of prey than morphological techniques. However, comparison with 2 other studies using similar molecular techniques suggests that all 5 species in our study fed nestlings a high diversity of prey (17−37 families in 5−18 samples) compared with the Western Bluebird (*Sialia mexicana*; 27 families in 169 fecal samples; Jedlicka et al. 2017) and the Louisiana Waterthrush (*Parkesia motacilla*; 41 families in 123 fecal samples; Trevelline et al. 2016).

Although all 5 species in our study had highly generalist diets, we found that Lapland Longspur, American Tree Sparrow, and Savannah Sparrow had the most diverse nestling diets, suggesting these species may be better able to cope with a changing food supply and thus less vulnerable to trophic mismatch. These 3 species also have larger geographic ranges than Golden-crowned Sparrow or Gray-cheeked Thrush (Norment et al. 1998, Lowther et al. 2001, Hussell and Montgomerie 2002, Wheelwright and Rising 2008, Naugler et al. 2017), and at the

population level range size is correlated with niche breadth in a wide range of taxa (Dapporto and Dennis 2013, Slatyer et al. 2013).

Given the wide temporal availability of common prey items and the high degree of generalization (Figures 3.3 and 3.4), we suspect that our focal species have low vulnerability to trophic mismatch. With continued climate change, prey phenology is expected to advance because temperature is the most important influence on arthropod development (Gilbert and Raworth 2000, Høye and Forchhammer 2008, Tulp and Schekkerman 2008). In contrast, many other factors influence the breeding phenology of migratory birds, including photoperiod, weather conditions, food supply, and social factors, some of which are unaffected by climate change (Visser et al. 2010, Helm et al. 2013, Davies and Deviche 2014). Therefore, it is expected that changes in arthropod phenology will be more rapid than shifts in passerine breeding phenology. Our findings of varied prey use between years, across the season, and over relatively short distances suggest that these birds can adjust to local availability. One of the most common prey items, dance flies (Empididae), reached peak abundance at the end of the passerine breeding season (Figure 3.3); therefore, a shift towards earlier availability may benefit birds in the short term. Further research is needed to determine how food availability and nesting chronology affect reproductive outcomes for generalist passerines in the Arctic.

We predict that, at least in the short term, vegetation shifts in response to climatic changes in the Arctic will benefit most passerines by increasing the overall abundance of arthropod prey. In our study area, abundance of Lepidoptera larvae is positively associated with willow (*Salix* spp.) cover, and abundance of both Empididae and Tenthredinidae larvae peaks when willow cover is about 60% (Chapter 2). This suggests that increases in willow in northwestern Alaska could increase food availability for our focal species, at least in the short

term. Increased growth of deciduous shrubs also provides nesting habitat more suitable for several passerines, such as the Gray-cheeked Thrush (Boelman et al. 2015, Thompson et al. 2016), and supports higher densities of nesting passerines in general (Sokolov et al. 2012). Thus, some passerines may benefit from increased nesting habitat as well as increased food availability with continued shrub expansion. Other species, such as the Lapland Longspur, are less tolerant of shrubs in nesting areas, and breeding densities are projected to decline in the future as a result of habitat loss (Thompson et al. 2016).

The Arctic passerines in our study fed their nestlings arthropod prey from all trophic levels, although herbivorous arthropods were consumed slightly more often. Many predaceous taxa were present in the diet, but since predaceous arthropods (Araneae, most Coleoptera in this study) were highly available, at least in pitfall traps, these birds appear to selectively feed herbivorous arthropods to their nestlings. Herbivorous arthropods were also found more frequently in NGS studies of nestling diet in agricultural systems, where it was suggested that birds may benefit crops by reducing abundance of pests (Crisol-Martinez et al. 2016, Jedlicka et al. 2017). Understanding such potential beneficial effects of insectivorous birds in tundra ecosystems would require more detailed quantification of adult and nestling diets, herbivorous arthropod abundance, and trophic interactions with plants.

Although all our study species are classified as ground-feeders, we found that nestling diets comprised primarily winged adult insects and larvae that live on vegetation. In agreement with many previous studies on passerine nestlings (Maher 1979, Biermann and Sealy 1982, Holmes and Schultz 1988), we found that Lepidoptera larvae were among the most frequently consumed prey and are an important resource for nestlings. Some caution is warranted in interpreting our results, as the arthropod primers used in our study preferentially amplified flies

(Diptera) and caterpillars over non-insect arthropods such as spiders (Araneae). Although we tried to limit this bias by using presence-absence metrics only, our data may underestimate the importance of non-insect invertebrates in nestling diet. Parasitoid taxa were observed in nestling diets (7 taxa in 5 of 60 fecal samples), although it is unclear whether parasitoids were captured directly or consumed incidentally while inside their hosts since we detected evidence to support both patterns.

If nestling diet comprises mostly flies and larvae, adult birds may glean more when provisioning their young than when foraging to feed themselves. Our field observations of adults support this (Figure 3.6). We had several observations of adult birds consuming ground beetles (Coleoptera: Carabidae) and spiders, but we never observed these large, chitinous arthropods carried in the bill as part of a food load delivered to nestlings. In several passerine species, nestling diet comprises more larvae and fewer hard-bodied arthropods than does the adult diet (Biermann and Sealy 1982, Moreno 1987, Orłowski et al. 2014, Jedlicka et al. 2017). The large size and high percentage of chitin in beetles and spiders may make them difficult for nestlings to consume and digest; this idea is supported by observations of some species in which parents remove chitinous heads and elytra of beetles when provisioning nestlings (Grundel and Dahlsten 1991).

Figure 3.6 Adult American Tree Sparrow carrying food to provision nestlings in northwestern Alaska, USA. Bill load is primarily composed of larvae (Lepidoptera: Geometridae and Hymenoptera: Tenthredinidae). Photo: M. McDermott

For 3 species (American Tree Sparrow, Golden-crowned Sparrow, and Gray-cheeked

Thrush), our study provides the first quantification of nestling diet and, for all 5 species, the first information on nestling diet using genetic methods. Although NGS still has some limitations, we were able to reveal prey use in these 5 species without using invasive techniques or morphological methods that may be biased against detection of soft-bodied prey, which appear to be particularly important in nestling diet. We found a remarkably high degree of generalization and flexibility in diet composition that suggests these Arctic passerines may be able to adjust to temporal and spatial variation in prey availability. To address potential effects of phenological mismatch on generalist insectivores, future research should focus on reproductive consequences of this variation in prey availability and resulting variation in diet composition. To uncover potential feedbacks on shrub expansion and further our understanding of songbirds in Arctic communities, we recommend that future research on nestling diet focus on quantifying the relative consumption of herbivorous and predaceous arthropods in Arctic songbird diet.

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3.7 APPENDICES

Appendix 3-A

Arthropod CO1 Sequencing Protocol
Updated August 2016 by Jonah Ventures

gDNA extraction
0.25g of sample was used for gDNA extraction using MoBio PowerSoil Kit (cat#12955) according to the manufacturer's protocol.

PCR
Primers used for Arthropod CO1 sequencing
Forward – 5' AGATATTGGAACWTTATATTTTATTTTTGG 3'
Reverse – 5'WACTAATCAATTWCCAAATCCTCC 3'

Target-specific PCR reaction (per rxn) – Arthropod CO1
12.5ul Mastermix (Promega cat # M5133)
1ul Forward primer (0.4uM final)
1ul Reverse primer (0.4uM final)
3ul gDNA
7.5 ul DNase/RNase-free H2O

Arthropod CO1 Cycling
94C – 5 minutes
94C – 30 seconds
45C- 45 seconds
72C – 45 seconds
x 45 cycles
72C – 10 minutes
10C - ∞

Agarose gel
Visualize 5ul PCR sample on a 2% agarose gel

PCR Clean Up
20ul of 1st step PCR amplicon was used for PCR clean-up using ExoI/SAP reaction.
8.85ul water, 0.023ul ExoI, 0.2275ul SAP was added to each PCR reaction and incubated 37C for 30 minutes. ExoI/SAP were then inactivated by incubation at 95C for 5 minutes.

Indexing PCR reaction (per rxn)
20ul Mastermix
2ul Forward Barcoded primer (0.5uM final)
2ul Universal Reverse primer (0.5uM final)
4ul template
12 ul DNase/RNase-free H2O

Indexing PCR Cycling

95C – 3 minutes
95C – 30 seconds
55C- 30 seconds
72C – 30 seconds
x 8 cycles
72C – 2 minutes
10C - ∞

Agarose gel

Visualize 5ul PCR sample on a 2% agarose gel. Amplicon should be ~80bp longer due to Indexing addition.

Normalization and Pooling

25ul of PCR amplicon was purified and normalize using the Life Technologies SequalPrep Normalization kit (cat#A10510-01) according to the manufacturer's protocol. Samples were then pooled together.

Sequencing

Amplicons were sequenced using an Illumina MiSeq housed in the CU Boulder BioFrontiers Sequencing Center using the v2 500-cycle kit (cat# MS-102-2002).

Sequence Processing

The following summarizes how the CO1 amplicons were processed via a joint QIIME (Caporaso et al. 2010) and UPARSE (Edgar 2013) pipeline similar to that of (Andrei et al. 2015), with modification. Sequences were demultiplexed by taking advantage of Golay barcodes (Caporaso et al. 2012) via QIIME v1.9.1 (Caporaso et al. 2010). The following options were used to output raw unfiltered fastq files for both forward and reverse reads: split_libraries_fastq.py -q 0 --max_bad_run_length 250 --min_per_read_length_fraction 0.0001 --sequence_max_n 250 --store_demultiplexed_fastq… . Primer sequences were trimmed using cutadapt [5] in 'paired-end mode' to remove the primers ZBJ-ArtF1c (5'-AGATATTGGAACWTTATATTTTATTTTTGG-3') and ZBJ-ArtR2c (5'-WACTAATCAATTWCCAAATCCTCC-3') (Zeale et al. 2011). Trimmed paired-ends where then merged by the –fastq_mergepairs option of usearch (Edgar 2010). From here, the general quality filtering and OTU construction was completed as per the UPARSE pipeline (Edgar 2013), with the following modifications: OTUs were generated by clustering the reads at 99% sequence similarity, reference based chimera removal was performed using the -uchime_ref command against a SINTAX (Edgar 2016) formatted reference database containing CO1 sequences downloaded from BOLD (Ratnasingham and Hebert 2007) using –minh 1.5. The OTU table was generated by mapping quality filtered reads back to the OTU seeds via an exhaustive search by setting the following –usearch_global parameters: -maxaccepts 0 -maxrejects 0. These parameters help to ensure that individual reads are mapped to their best matching OTU seeds. Taxonomy was assigned by using the SINTAX (Edgar 2016) protocol of usearch (Edgar 2010).

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Appendix 3-B

Assessment of Primer Bias

We retrieved usable sequence data from both replicates of invertebrate tissue. There was a high degree of consistency among replicates, with similar percentage of reads from each taxonomic group (Figure 3-B.1). Results indicate little bias in the extraction and preparation of each sample, but significant taxonomic bias of the primers used. Diptera (flies), Lepidoptera (moths and caterpillars) and Psocodea (book lice) were amplified well. Coleoptera (beetles) and Hemiptera (true bugs) were amplified moderately well. Amplification was poor for Hymenoptera

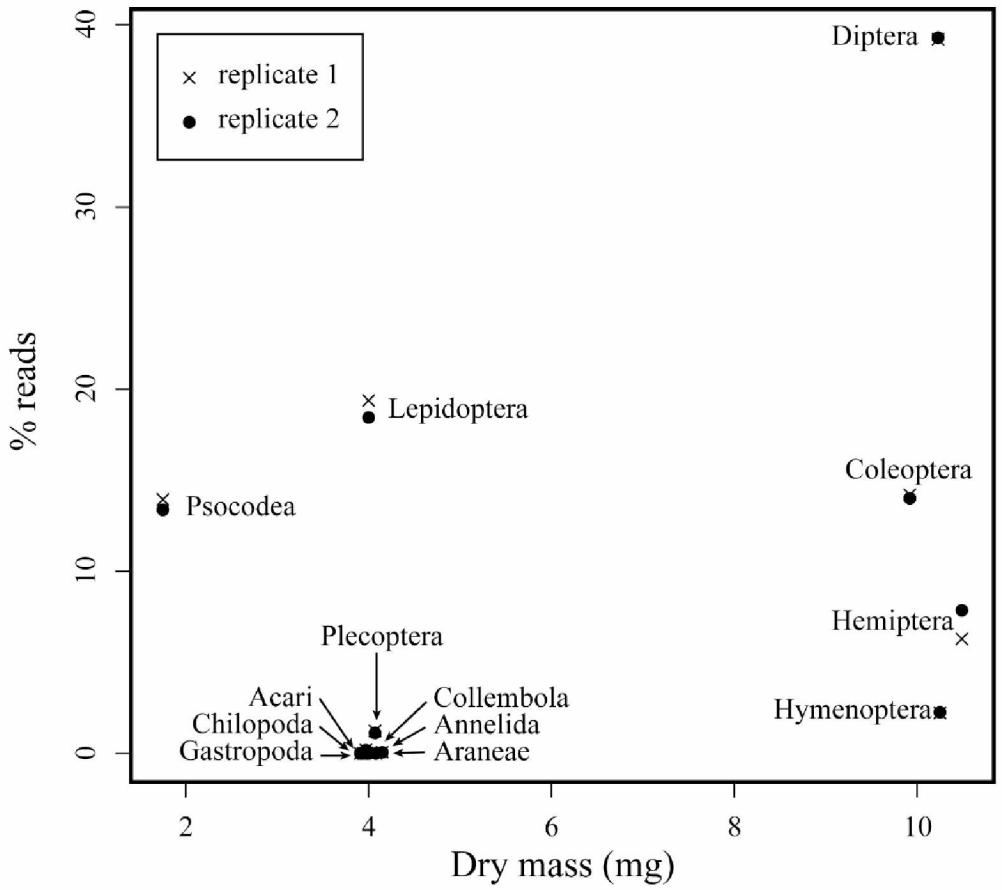

Figure 3-B.1 Arthropod sample sequencing results showing the % of reads recovered for each order relative to the amount of dry mass in each sample. Extraction and sequencing protocol was performed twice on the same mixture of arthropod tissue, with high concordance.

(ants, bees, wasps, sawflies), Plecoptera (stoneflies), Acari (mites), Araneae (spiders), and Collembola (springtails), and no reads were recovered for non-arthropod invertebrates Annelida (worms), Chilopoda (centipedes), or Gastropoda (slugs and snails) (Figure 3-B.1). Again, these results reflect only the 2 arthropod tissue samples. Due to significant evidence of primer bias in amplification from this and other studies (Clarke et al. 2014; Pinol et al. 2015), we performed our analyses using presence-absence data only.

Appendix 3-C

Occurrence of Arthropod DNA in Nestling Fecal Matter

Table 3-C.1 Arthropod molecular operational taxonomic units (MOTUs) detected in 117 samples from 6 migratory arctic passerines in northwestern Alaska, 2015-2016. Numbers are the number of fecal samples where a given prey taxon was detected. ATSP = American Tree Sparrow, GCSP = Golden-crowned Sparrow, GCTH = Gray-cheeked Thrush, LALO = Lapland Longspur, SAVS = Savannah Sparrow, YWAR = Yellow Warbler.

Order	Family	Species	ATSP *n = 20*	GCSP *n = 33*	GCTH *n = 23*	LALO *n = 22*	SAVS *n = 15*	YWAR *n = 4*
Amphipoda	Corophiidae	*Monocorophium acherusicum*	-	-	-	-	-	1
Araneae	Araneidae	*Araneus* sp.	1	1	-	-	-	-
		Araneus corticarius	-	-	-	-	1	-
	Clubionidae	*Clubiona* sp.	-	-	-	1	-	-
		Clubiona praematura	-	-	-	1	1	-
	Linyphiidae	*Unknown*	-	-	1	2	-	-
		Allomengea scopigera	-	-	1	-	-	-
		Bathyphantes brevipes	-	-	1	-	-	-
		Centromerus sylvaticus	-	-	1	-	-	-
		Collinsia holmgreni	-	-	-	1	-	-
		Estrandia grandaeva	4	-	1	-	-	-
		Hilaira sp.	-	1	-	-	-	-
		Hilaira herniosa	-	-	1	-	1	-
		Hypselistes florens	-	-	-	-	1	-
		Kaestneria pullata	-	1	-	-	1	-
		Lepthyphantes alpinus	-	1	-	-	-	-
		Microlinyphia sp.	-	-	-	1	-	-
		Oreoneta banffkluane	-	1	-	-	-	-
		Oreoneta leviceps	-	-	-	1	-	-
		Oreonetides vaginatus	-	-	-	1	-	-
	Lycosidae	*Pardosa* sp.	1	-	-	4	2	-

Table 3-C.1 cont.

Order	Family	Species
Araneae, cont.	Lycosidae, cont.	*Pardosa fuscula*
		Pardosa palustris
	Philodromidae	*Thanatus formicinus*
		Thanatus rubicellus
		Thanatus striatus
		Tibellus sp.
Coleoptera	Cantharidae	*Dichelotarsus flavimanus*
		Dichelotarsus puberulus
		Podabrus lapponicus
	Carabidae	*Unknown*
		Bembidion breve
		Diacheila polita
		Notiophilus borealis
		Pterostichus sp.
		Pterostichus pinguedineus
		Pterostichus sublaevis
	Chrysomelidae	*Chrysomela collaris*
	Curculionidae	*Lepidophorus lineaticollis*
	Leiodidae	*Catops alpinus*
	Silphidae	*Thanatophilus sagax*
	Staphylinidae	*Unknown*
		Olophrum latum
		Oxypoda opaca
		Tachinus elongatus
Diptera	Anthomyiidae	*Unknown*
		Delia echinata
		Lasiomma cuneicorne
		Lasiomma latipenne

ATSP	GCSP	GCTH	LALO	SAVS	YWAR
n = 20	*n = 33*	*n = 23*	*n = 22*	*n = 15*	*n = 4*
-	1	-	-	-	-
-	2	-	-	1	-
-	1	-	-	-	-
-	2	-	3	-	-
-	-	-	2	-	-
2	3	-	3	-	-
4	3	3	3	2	-
1	-	-	-	-	-
1	1	2	3	1	-
-	6	4	4	-	2
-	1	-	-	-	-
-	-	1	-	-	-
-	-	-	-	-	-
-	1	-	2	-	-
-	-	1	-	-	2
-	-	-	1	-	-
-	3	1	-	-	-
-	1	1	-	-	-
-	-	-	1	-	-
-	-	1	-	-	-
-	-	1	-	-	-
-	-	-	1	-	-
-	-	-	1	-	2
-	1	1	-	-	-
2	1	-	3	-	-
1	-	-	-	-	-
-	-	-	1	-	-
-	-	-	1	-	-

Table 3-C.1 cont.

Order	Family	Species
Diptera, cont.	Calliphoridae	*Lucilia* sp.
	Cecidomyiidae	*Unknown*
	Ceratopogonidae	*Unknown*
		Forcipomyia sp.
	Chironomidae	*Unknown*
		Chironomus sp. TE11
		Gymnometriocnemus brumalis
		Micropsectra insignilobus
		Pagastia sp.
		Paraphaenocladius impensus
		Paratanytarsus sp.
		Procladius cf. ruris
		Pseudodiamesa sp.
		Pseudorthocladius curtistylus
		Rheocricotopus robacki
		Smittia sp.
		Thienemannimyia sp. 1ES
		Tvetenia paucunca
	Culicidae	*Unknown*
		Culiseta sp.
	Cylindrotomidae	*Cylindrotoma distinctissima*
	Dolichopodidae	*Dolichopus armillatus*
		Dolichopus nigrilineatus
		Dolichopus rupestris
	Empididae	*Unknown*
		Empis sp.
		Empis lucida
		Hilara sp.

ATSP	GCSP	GCTH	LALO	SAVS	YWAR
n = 20	*n = 33*	*n = 23*	*n = 22*	*n = 15*	*n = 4*
-	-	-	-	1	-
-	1	-	-	-	-
1	-	-	-	-	-
-	2	-	-	-	-
3	3	1	1	1	-
1	-	-	-	-	-
-	-	-	-	1	-
-	1	-	-	1	-
1	-	-	-	-	-
1	-	-	-	-	-
-	-	-	-	1	-
1	-	-	-	-	-
-	-	1	-	-	-
-	-	-	1	-	-
-	-	-	-	-	-
-	1	-	-	-	-
-	-	1	-	-	-
1	-	-	-	-	-
4	4	-	2	3	-
-	1	-	-	-	-
1	6	2	-	-	-
-	-	-	1	-	-
-	-	1	-	-	-
-	1	-	-	-	-
13	17	2	9	6	-
7	5	2	7	5	1
9	11	2	4	5	1
8	5	7	1	3	1

Table 3-C.1 cont.

Order	Family	Species
Diptera, cont.	Empididae, cont.	*Iteaphila nitidula*
		Rhamphomyia sp.
		Rhamphomyia fuscipennis
		Rhamphomyia pusilla
	Fanniidae	*Fannia mollissima*
		Fannia subpellucens
	Hybotidae	*Bicellaria bisetosa*
	Keroplatidae	*Macrocera zetterstedti*
	Limoniidae	*Unknown*
		Dactylolabis rhicnoptiloides
		Dicranomyia sp.
		Molophilus sp.
	Muscidae	*Coenosia* sp.
		Coenosia comita
		Helina evecta
		Helina fulvisquama
		Phaonia alpicola
		Phaonia consobrina
		Phaonia hybrida
		Phaonia lugubris
		Spilogona sp.
		Thricops sp.
		Thricops coquilletti
		Thricops villicrus
	Mycetophilidae	*Unknown*
		Boletina sp.
		Boletina pectiunguis
		Mycomya sp.

ATSP	GCSP	GCTH	LALO	SAVS	YWAR
n = 20	*n = 33*	*n = 23*	*n = 22*	*n = 15*	*n = 4*
-	1	-	-	1	-
13	18	4	9	10	4
-	-	-	1	-	-
-	-	-	2	-	-
-	1	-	-	-	-
-	-	1	-	-	-
1	-	-	-	1	-
-	3	-	-	-	-
-	-	1	1	-	-
-	-	-	-	1	-
-	-	-	1	-	-
-	-	1	-	-	-
1	2	-	1	-	-
-	-	1	-	-	-
-	-	-	-	1	-
3	1	1	-	-	-
-	1	-	-	1	-
1	-	1	1	-	-
1	-	-	-	-	-
-	-	-	1	-	-
-	-	-	1	-	-
2	-	1	-	-	-
1	-	-	-	-	-
-	-	1	-	-	-
-	1	-	-	-	-
-	1	-	-	-	-
-	1	-	-	-	-
2	1	-	-	1	-

Table 3-C.1 cont.

Order	Family	Species
Diptera, cont.	Pediciidae	*Unknown*
	Pipunculidae	*Cephalops* sp.
		Tomosvaryella sp.
	Rhagionidae	*Unknown*
		Ptiolina majuscula
	Simuliidae	*Helodon pleuralis*
	Syrphidae	*Eupeodes* sp.
		Melangyna sp.
		Melanostoma sp.
		Parasyrphus sp.
		Parasyrphus tarsatus
		Platycheirus sp.
		Platycheirus angustatus
		Platycheirus hyperboreus
		Platycheirus setitarsis
		Sphaerophoria sp.
	Tachinidae	*Unknown*
		Blepharomyia pagana
		Chrysoexorista sp.
		Ramonda ringdahli
	Tipulidae	*Unknown*
		Angarotipula tumidicornis
		Prionocera sp.
		Tipula
Ephemeroptera	Ephemerellidae	*Ephemerella aurivillii*
Hemiptera	Anthocoridae	*Anthocoris tomentosus*
	Aphididae	*Euceraphis borealis*
	Cicadellidae	*Unknown*

ATSP *n = 20*	GCSP *n = 33*	GCTH *n = 23*	LALO *n = 22*	SAVS *n = 15*	YWAR *n = 4*
-	1	-	-	-	-
-	1	-	-	-	-
-	-	-	1	-	-
-	-	-	4	2	-
3	2	-	-	-	-
2	-	-	-	-	-
1	-	1	-	-	-
-	-	1	-	-	-
1	3	1	5	1	-
2	1	-	-	1	-
1	1	-	-	2	-
2	7	1	1	1	-
-	1	-	-	-	-
-	1	-	-	-	-
-	2	-	-	-	-
2	1	-	-	-	-
-	1	-	-	-	-
1	-	-	-	-	-
-	1	-	-	-	-
-	2	-	-	-	-
-	1	2	2	-	-
1	-	-	1	-	-
-	-	-	1	-	-
2	4	16	3	2	-
1	-	-	-	-	-
-	-	1	-	-	-
5	-	-	-	-	-
-	1	-	6	-	-

Table 3-C.1 cont.

Order	Family	Species
Hemiptera, cont.	Cicadellidae, cont.	*Sorhoanus* sp.
		Stroggylocephalus placidus
	Miridae	*Lygocoris rugicollis*
		Lygus sp.
	Miridae	*Unknown*
	Psyllidae	*Unknown*
		Cacopsylla sp.
Hymenoptera	Braconidae	*Protapanteles sp.*
	Cimbicidae	*Trichiosoma lucorum*
	Encyrtidae	*Copidosoma floridanum*
	Ichneumonidae	*Unknown*
		Agrypon flaveolatum
		Campoletis sp.
		Cratichneumon sp.
		Enytus montanus
		Polyblastus sp.
		Smicroplectrus sp.
	Platygastridae	*Unknown*
	Proctotrupidae	*Proctotrupes bistriatus*
	Tenthredinidae	*Unknown*
		Amauronematus sp.
		Amauronematus fallax
		Amauronematus krausi
		Amauronematus miltonotus
		Amauronematus neglectus
		Amauronematus nitidipleuris
		Cladius sp.
		Cladius pallipes

ATSP *n = 20*	GCSP *n = 33*	GCTH *n = 23*	LALO *n = 22*	SAVS *n = 15*	YWAR *n = 4*
1	-	-	-	-	-
2	1	-	-	-	-
1	-	-	-	-	1
-	2	-	1	-	-
-	2	1	1	3	-
4	1	1	1	2	3
-	2	2	-	1	2
-	-	1	-	-	-
1	1	-	1	2	2
-	2	-	-	-	-
1	1	2	3	-	-
-	-	1	-	-	-
-	1	-	-	-	-
-	1	-	-	-	-
-	1	1	-	-	-
-	-	1	-	-	-
-	-	1	-	-	-
-	-	-	1	-	-
-	-	-	1	-	-
5	6	6	5	5	2
9	1	6	4	1	1
-	-	1	-	-	-
2	-	2	-	-	1
-	2	10	-	-	-
1	-	-	-	-	-
-	-	1	-	-	1
1	1	-	1	-	-
2	-	-	-	-	-

Table 3-C.1 cont.

Order	Family	Species
Hymenoptera, cont.	Tenthredinidae, cont.	*Dolerus yukonensis*
		Empria sp.
		Euura sp.
		Hemichroa crocea
		Nematus sp.
		Nematus poecilonotus
		Pachynematus sp.
		Pachynematus vagus
		Pristiphora sp.
		Pristiphora borea
		Pristiphora lativentris
		Pristiphora mollis
		Tenthredo arctica
Lepidoptera	Depressariidae	*Agonopterix gelidella*
	Elachistidae	*Elachista sp.*
	Erebidae	*Gynaephora rossii*
		Pararctia subnebulosa
	Geometridae	*Unknown*
		Dysstroma sp.
		Epirrhoe hastulata
		Epirrita sp.
		Eulithis sp.
		Eupithecia lariciata
		Hydriomena sp.
		Hydriomena furcata
		Operophtera sp.
		Operophtera bruceata
		Speranza brunneata

ATSP	GCSP	GCTH	LALO	SAVS	YWAR
n = 20	*n = 33*	*n = 23*	*n = 22*	*n = 15*	*n = 4*
-	-	2	-	1	-
-	2	-	-	-	-
-	-	1	-	-	-
-	-	3	-	-	-
6	1	11	2	2	2
1	-	-	-	-	-
-	4	1	3	1	-
1	1	-	3	2	-
3	6	6	4	5	1
-	-	-	1	-	-
5	2	1	3	4	3
-	-	-	1	-	-
-	-	-	1	-	-
-	-	-	3	-	-
-	-	-	1	-	-
-	-	1	1	-	-
-	2	-	-	-	-
4	-	-	1	1	-
-	-	1	-	-	-
-	1	-	-	-	-
1	-	1	-	-	-
5	11	10	5	6	3
-	-	-	1	-	-
-	3	2	1	3	-
2	4	10	1	5	2
12	9	7	12	7	1
-	-	-	-	-	-
8	10	-	5	2	-

Table 3-C.1 cont.

Order	Family	Species
Lepidoptera, cont.	Geometridae, cont.	*Xanthorhoe fossaria*
		Xanthorhoe labradorensis
	Incurvariidae	*Incurvaria vetulella*
	Noctuidae	*Unknown*
		Apamea lintneri
		Autographa pseudogamma
		Sunira verberata
		Sympistis sp.
		Sympistis funebris
		Syngrapha sp.
		Syngrapha diasema
		Syngrapha parilis
		Xestia albuncula
	Nymphalidae	*Unknown*
		Boloria sp.
		Boloria frigga
		Erebia sp.
		Erebia rossii
		Oeneis sp.
	Papilionidae	*Papilio machaon*
	Schreckensteiniidae	*Schreckensteinia festaliella*
	Tortricidae	*Unknown*
		Acleris sp.
		Acleris cf emargana
		Aethes monera
		Ancylis sp.
		Ancylis myrtillana
		Ancylis uncella

ATSP	GCSP	GCTH	LALO	SAVS	YWAR
n = 20	*n = 33*	*n = 23*	*n = 22*	*n = 15*	*n = 4*
-	-	3	-	-	-
1	-	-	-	-	-
-	-	1	-	-	-
-	-	5	1	-	-
-	2	-	1	-	-
-	-	2	-	-	-
-	-	1	-	-	-
-	1	-	-	-	-
1	-	-	-	2	-
2	4	-	3	2	-
1	1	1	-	-	-
-	-	-	1	-	-
1	-	-	-	-	-
-	-	-	1	-	-
-	-	-	2	-	-
-	-	-	1	-	-
-	1	-	-	-	-
-	1	-	-	-	-
-	-	-	1	-	-
-	1	-	-	-	-
-	1	-	-	-	-
-	-	-	1	-	-
1	-	3	-	-	-
-	-	1	-	-	-
-	-	1	-	-	-
-	1	-	-	1	-
-	1	-	-	-	-
-	1	-	-	-	-

Table 3-C.1 cont.

Order	Family	Species	ATSP *n = 20*	GCSP *n = 33*	GCTH *n = 23*	LALO *n = 22*	SAVS *n = 15*	YWAR *n = 4*
Lepidoptera, cont.	Tortricidae, cont.	*Aphelia sp.*	-	-	-	3	-	-
		Apotomis sp.	-	-	-	1	-	-
		Epinotia sp.	-	3	-	1	-	-
		Epinotia myricana	2	-	-	1	-	-
		Epinotia trigonella	5	-	-	2	-	-
		Grapholita aureolana	-	-	-	1	-	-
		Olethreutes sp.	-	-	-	1	-	-
	Ypsolophidae	*Ypsolopha sp.*	1	-	-	-	-	-
Neuroptera	Hemerobiidae	*Hemerobius sp.*	-	-	-	-	-	-
		Hemerobius ovalis	-	-	1	-	-	-
		Wesmaelius sp.	1	-	1	-	-	-
		Wesmaelius nervosus	1	-	-	-	2	-
Orthoptera	Acrididae	*Aeropedellus clavatus*	-	-	1	-	-	-
Plecoptera	Capniidae	*Capnia coloradensis*	-	-	-	-	-	-
	Chloroperlidae	*Alloperla serrata*	-	-	1	-	-	-
Psocodea	Caeciliusidae	*Valenzuela flavidus*	-	-	-	-	-	-
Symphypleona	Sminthuridae	*Unknown*	-	-	-	-	1	-
Trichoptera	Glossosomatidae	*Glossosoma intermedium*	-	-	1	-	-	-
	Limnephilidae	*Arctopora pulchella*	2	-	-	-	-	-
		Lenarchus productus	-	-	1	-	-	-
		Limnephilus sp.	-	-	1	-	-	-
		Limnephilus diphyes	-	-	-	-	1	-

Table 3-C.2 Arthropod molecular operational taxonomic units (MOTUs) detected in 60 fecal samples from 5 migratory arctic passerines in northwestern Alaska, 2015-2016. Numbers are the number of fecal samples where a given prey taxon was detected. Guild designations are based on the life stage most likely in the diet, e.g., Tenthredinidae are listed as herbivores even though adults are predaceous, since field observations and stomach samples found only larval stages in the diet. ATSP = American Tree Sparrow, GCSP = Golden-crowned Sparrow, GCTH = Gray-cheeked Thrush, LALO = Lapland Longspur, SAVS = Savannah Sparrow.

				ATSP	GCSP	GCTH	LALO	SAVS
Order	Family	Species	Guild[1]	*n = 8*	*n = 18*	*n = 12*	*n = 17*	*n = 5*
Araneae	Araneidae	*Araneus* sp.	P	-	1	-	-	-
		Araneus corticarius	P	-	-	-	-	1
		Hypsosinga albovittata	P	-	-	-	1	-
	Clubionidae	*Clubiona* sp.	P	-	-	-	1	-
		Clubiona praematura	P	-	-	-	1	-
	Linyphiidae	Unknown	P	-	-	-	1	-
		Allomengea scopigera	P	-	-	1	-	-
		Centromerus sylvaticus	P	-	-	1	-	-
		Collinsia holmgreni	P	-	-	-	1	-
		Estrandia grandaeva	P	1	-	1	-	-
		Kaestneria pullata	P	-	-	-	-	1
		Lepthyphantes alpinus	P	-	1	-	-	-
		Microlinyphia sp.	P	-	-	-	1	-
		Oreoneta banffkluane	P	-	1	-	-	-
		Oreoneta leviceps	P	-	-	-	1	-
		Oreonetides vaginatus	P	-	-	-	1	-
	Lycosidae	*Pardosa* sp.	P	-	-	-	3	-
		Pardosa palustris	P	-	2	-	-	1
	Philodromidae	*Thanatus formicinus*	P	-	1	-	-	-
		Thanatus rubicellus	P	-	-	-	4	-
		Thanatus striatus	P	-	-	-	1	-
		Tibellus sp.	P	-	1	-	3	-

Table 3-C.2, cont.

Order	Family	Species
Coleoptera	Cantharidae	*Dichelotarsus flavimanus*
		Dichelotarsus puberulus
		Podabrus lapponicus
	Carabidae	Unknown
		Diacheila polita
		Pterostichus sp.
		Pterostichus sublaevis
	Chrysomelidae	*Chrysomela collaris*
	Curculionidae	*Lepidophorus lineaticollis*
	Leiodidae	*Catops alpinus*
	Staphylinidae	*Olophrum latum*
		Oxypoda opaca
Diptera	Anthomyiidae	Unknown
		Lasiomma cuneicorne
		Lasiomma latipenne
	Calliphoridae	*Lucilia* sp.
	Ceratopogonidae	*Forcipomyia* sp.
	Chironomidae	Unknown
		Chironomus sp. TE11
		Gymnometriocnemus brumalis
		Micropsectra insignilobus
		Paraphaenocladius impensus
		Paratanytarsus sp.
		Pseudodiamesa sp.
		Smittia sp.
		Thienemannimyia sp. 1ES
		Tvetenia paucunca

Guild[1]	ATSP *n = 8*	GCSP *n = 18*	GCTH *n = 12*	LALO *n = 17*	SAVS *n = 5*
P	2	1	1	2	1
P	1	-	-	-	-
P	-	-	-	3	-
	-	1	2	3	-
P	-	-	1	-	-
P	-	-	-	1	-
P	-	-	-	1	-
H	-	1	-	-	-
H	-	-	1	-	-
DSF	-	-	-	1	-
P	-	-	-	1	-
P	-	-	-	1	-
	1	-	-	1	1
H	-	-	-	1	-
H	-	-	-	1	-
DSF*	-	-	-	-	1
PS*	-	2	-	-	-
	2	2	-	1	1
NF	1	-	-	-	-
NF	-	-	-	-	1
NF	-	-	-	-	1
NF	1	-	-	-	-
NF	-	-	-	-	1
NF	-	-	1	-	-
NF	-	1	-	-	-
NF	-	-	1	-	-
NF	-	-	-	-	1

Table 3-C.2, cont.

Order	Family	Species
Diptera, cont.	Culicidae	Unknown
		Culiseta sp.
	Cylindrotomidae	*Cylindrotoma distinctissima*
	Dolichopodidae	*Dolichopus armillatus*
		Dolichopus rupestris
	Empididae	Unknown
		Empis sp.
		Empis lucida
		Hilara sp.
		Rhamphomyia sp.
		Rhamphomyia fuscipennis
		Rhamphomyia pusilla
	Hybotidae	*Bicellaria bisetosa*
	Keroplatidae	*Macrocera zetterstedti*
	Limoniidae	*Dicranomyia* sp.
		Molophilus sp.
	Muscidae	*Coenosia* sp.
		Helina fulvisquama
		Phaonia consobrina
		Phaonia lugubris
		Spilogona sp.
	Mycetophilidae	*Boletina* sp.
		Mycomya sp.
	Rhagionidae	Unknown
		Ptiolina majuscula
	Scathophagidae	Unknown
	Syrphidae	*Cheilosia bigelowi*

Guild[1]	ATSP *n = 8*	GCSP *n = 18*	GCTH *n = 12*	LALO *n = 17*	SAVS *n = 5*
	2	4	-	1	2
O*	-	1	-	-	-
NF	-	3	-	-	-
P	-	-	-	1	-
P	-	1	-	-	-
P	3	8	-	9	2
P	1	2	2	5	1
P	2	4	-	4	2
P	3	2	3	-	1
P	4	10	-	6	5
P	-	-	-	1	-
P	-	-	-	1	-
P	1	-	-	-	-
O	-	1	-	-	-
NF	-	-	-	1	-
NF	-	-	1	-	-
P	1	-	-	-	-
H	1	1	-	-	-
H	-	-	-	1	-
H	-	-	-	1	-
H	-	-	-	1	-
DSF	-	1	-	-	-
DSF	2	-	-	-	-
P	-	-	-	1	-
P	2	1	-	-	-
	-	-	-	1	-
O*	-	1	-	-	-

Table 3-C.2, cont.

Order	Family	Species
Diptera, cont.	Syrphidae, cont.	*Eupeodes* sp.
		Melanostoma sp.
		Parasyrphus sp.
		Parasyrphus tarsatus
		Platycheirus sp.
		Platycheirus hyperboreus
		Sphaerophoria sp.
	Tachinidae	Unknown
		Chrysoexorista sp.
	Tipulidae	Unknown
		Angarotipula tumidicornis
		Prionocera sp.
		Tipula sp.
Hemiptera	Anthocoridae	*Anthocoris tomentosus*
	Aphididae	*Euceraphis borealis*
	Cicadellidae	Unknown
		Sorhoanus sp.
		Stroggylocephalus placidus
	Miridae	Unknown
		Lygus sp.
	Psyllidae	Unknown
		Cacopsylla sp.
Hymenoptera	Braconidae	*Protapanteles* sp.
	Cimbicidae	*Trichiosoma lucorum*
	Encyrtidae	*Copidosoma floridanum*
	Ichneumonidae	Unknown
		Campoletis sp.

Guild[1]	ATSP *n = 8*	GCSP *n = 18*	GCTH *n = 12*	LALO *n = 17*	SAVS *n = 5*
O*	1	-	-	-	-
O*	-	-	-	4	-
O*	1	-	-	-	-
O*	1	-	-	-	1
O*	2	4	1	1	1
O*	-	1	-	-	-
O*	1	1	-	-	-
PS	-	1	-	-	-
PS	-	1	-	-	-
NF	-	-	1	1	-
NF	1	-	-	1	-
NF	-	-	-	1	-
NF	2	2	7	3	1
P	-	-	1	-	-
H	1	-	-	-	-
H	-	-	-	4	-
H	1	-	-	-	-
H	1	1	-	-	-
H	-	2	-	-	-
H	-	-	-	1	-
H	3	1	1	1	-
H	1	2	2	-	1
PS	-	-	1	-	-
H	1	1	-	-	-
PS	-	1	-	-	-
PS	-	-	1	1	-
PS	-	1	-	-	-

Table 3-C.2, cont.

Order	Family	Species
Hymenoptera, cont.	Ichneumonidae, cont.	*Polyblastus* sp.
	Platygastridae	*Platygastridae*
	Proctotrupidae	*Proctotrupes bistriatus*
	Tenthredinidae	Unknown
		Amauronematus sp.
		Amauronematus fallax
		Amauronematus krausi
		Amauronematus miltonotus
		Cladius sp.
		Dolerus yukonensis
		Empria sp.
		Nematus sp.
		Pachynematus sp.
		Pachynematus vagus
		Pristiphora sp.
		Pristiphora lativentris
		Tenthredo arctica
Lepidoptera	Depressariidae	*Agonopterix gelidella*
	Elachistidae	*Elachista* sp.
	Erebidae	*Gynaephora rossii*
	Geometridae	Unknown
		Epirrhoe hastulata
		Eulithis sp.
		Eupithecia lariciata
		Hydriomena sp.
		Hydriomena furcata
		Operophtera sp.

Guild[1]	ATSP *n = 8*	GCSP *n = 18*	GCTH *n = 12*	LALO *n = 17*	SAVS *n = 5*
PS	-	-	1	-	-
PS	-	-	-	1	-
PS	-	-	-	1	-
H	1	3	1	2	1
H	2	1	2	4	-
H	-	-	1	-	-
H	-	-	1	-	-
H	1	1	4	-	-
H	-	-	-	1	-
H	-	-	2	-	-
H	-	1	-	-	-
H	2	-	5	2	-
H	-	2	-	2	1
H	-	-	-	2	1
H	1	2	2	2	-
H	1	1	-	1	1
H	-	-	-	1	-
H	-	-	-	3	-
H	-	-	-	1	-
H	-	-	-	1	-
H	2	-	-	1	1
H	-	1	-	-	-
H	3	4	7	6	2
H	-	-	-	1	-
H	-	-	-	1	1
H	1	1	5	1	2
H	5	3	3	11	2

Table 3-C.2, cont.

Order	Family	Species
Lepidoptera, cont.	Geometridae, cont.	*Speranza brunneata*
		Xanthorhoe fossaria
		Xanthorhoe labradorensis
	Lycaenidae	Unknown
	Noctuidae	Unknown
		Apamea lintneri
		Sympistis sp.
		Sympistis funebris
		Syngrapha sp.
		Xestia albuncula
	Nymphalidae	Unknown
		Boloria sp.
		Boloria frigga
		Erebia sp.
	Papilionidae	*Papilio machaon*
	Tortricidae	Unknown
		Acleris sp.
		Ancylis sp.
		Aphelia sp.
		Clepsis moeschleriana
		Epinotia sp.
		Epinotia myricana
		Epinotia trigonella
		Grapholita aureolana
		Olethreutes sp.
	Ypsolophidae	*Ypsolopha* sp.

Guild[1]	ATSP *n = 8*	GCSP *n = 18*	GCTH *n = 12*	LALO *n = 17*	SAVS *n = 5*
H	3	5	-	5	-
H	-	-	1	-	-
H	1	-	-	-	-
H	-	-	-	1	-
H	-	-	1	-	-
H	-	2	-	1	-
H	-	1	-	-	-
H	-	-	-	-	2
H	-	1	-	3	1
H	-	-	-	1	-
H	-	-	-	1	-
H	-	-	-	1	-
H	-	-	-	1	-
H	-	1	-	-	-
H	-	1	-	-	-
H	-	-	-	1	-
H	-	-	1	-	-
H	-	1	-	-	1
H	-	-	-	2	-
H	-	-	-	1	-
H	-	1	-	1	-
H	-	-	-	1	-
H	1	1	-	1	-
H	-	-	-	1	-
H	-	-	-	1	-
H	1	-	-	-	-

Table 3-C.2, cont.

Order	Family	Species	Guild[1]	ATSP *n = 8*	GCSP *n = 18*	GCTH *n = 12*	LALO *n = 17*	SAVS *n = 5*
Neuroptera	Hemerobiidae	*Hemerobius* sp.	P	-	-	-	1	-
		Hemerobius ovalis	P	-	-	1	-	-
Plecoptera	Chloroperlidae	*Alloperla serrata*	NF	-	-	1	-	-
Symphypleona	Sminthuridae	Unknown		-	-	-	-	1
Trichoptera	Limnephilidae	*Arctopora pulchella*	NF	2	-	-	-	-
		Lenarchus productus	NF	-	-	1	-	-
		Limnephilus sp.	NF	-	1	1	-	-

[1] P = Predator, H = Herbivore, NF = Non-feeding, O = Omnivore, PS = Parasitoid, DSF = Detritivore, Scavenger, and/or Fungivore

Appendix 3-D
IACUC Approval (Protocol 731880)

Please note that University of Alaska Fairbanks IACUC has taken the following action on IRBNet:

Project Title: [731880-3] Dynamics of Food Availability for Tundra-nesting Passerines in Western Alaska
Principal Investigator: Pat Doak, Ph.D.

Submission Type: Amendment/Modification
Date Submitted: May 7, 2015

Action: APPROVED
Effective Date: May 13, 2015
Review Type: Designated Member Review

Should you have any questions you may contact Gretchen Hundertmark at ghundertmark@alaska.edu.

Thank you,
The IRBNet Support Team

Appendix 3-E
US Fish and Wildlife Service Federal Permit

DEPARTMENT OF THE INTERIOR
U.S. FISH AND WILDLIFE SERVICE
Migratory Bird Permit Office
1011 E. Tudor Rd (MS-201) - Anchorage, AK 99503
Tel: 907-786-3693 Fax: 907-786-3927
Email: permitsR7MB@fws.gov

FEDERAL FISH AND WILDLIFE PERMIT

1. PERMITTEE

U.S. GEOLOGICAL SURVEY
dba ALASKA BIOLOGICAL SCIENCE CENTER
ATTN: JOHN PEARCE
4210 UNIVERSITY DRIVE
ANCHORAGE, AK 99508
U.S.A.

2. AUTHORITY-STATUTES
16 USC 703-712
16 USC 1538(f)

REGULATIONS
50 CFR PART 13
50 CFR 21.23
50 CFR 21.21
50 CFR 14.31

3. NUMBER
MB789758-0

4. RENEWABLE
[X] YES
[ ] NO

5. MAY COPY
[X] YES
[ ] NO

6. EFFECTIVE
04/01/2015

7. EXPIRES
03/31/2018

8. NAME AND TITLE OF PRINCIPAL OFFICER *(If #1 is a business)*
JOHN PEARCE
CHIEF, WETLANDS & TERRESTIAL ECOLOGY

9. TYPE OF PERMIT
SCIENTIFIC COLLECTING WITH IMPORT/EXPORT AND PORT EXCEPTION

10. LOCATION WHERE AUTHORIZED ACTIVITY MAY BE CONDUCTED

Scientific collecting authority for locations in ALASKA as described below.
Import/export authority through all ports designated under 50 CFR 14.12 and through the non-designated ports of FAIRBANKS,

11. CONDITIONS AND AUTHORIZATIONS:

A. GENERAL CONDITIONS SET OUT IN SUBPART D OF 50 CFR 13, AND SPECIFIC CONDITIONS CONTAINED IN FEDERAL REGULATIONS CITED IN BLOCK #2 ABOVE, ARE HEREBY MADE A PART OF THIS PERMIT. ALL ACTIVITIES AUTHORIZED HEREIN MUST BE CARRIED OUT IN ACCORD WITH AND FOR THE PURPOSES DESCRIBED IN THE APPLICATION SUBMITTED. CONTINUED VALIDITY, OR RENEWAL, OF THIS PERMIT IS SUBJECT TO COMPLETE AND TIMELY COMPLIANCE WITH ALL APPLICABLE CONDITIONS, INCLUDING THE FILING OF ALL REQUIRED INFORMATION AND REPORTS.

B. THE VALIDITY OF THIS PERMIT IS ALSO CONDITIONED UPON STRICT OBSERVANCE OF ALL APPLICABLE FOREIGN, STATE, LOCAL, TRIBAL, OR OTHER FEDERAL LAW.

C. VALID FOR USE BY PERMITTEE NAMED ABOVE.

D. You are authorized to take, transport, and possess the following migratory birds for scientific purposes:

1. Examination of bill deformities in black-capped chickadees and forest birds.
Location: State of Alaska
Date of activities: January - December
Project Leader: Colleen Handel
Additional Project Personnel: Lisa Pajot and Caroline Van Hemert.
Authorized Activities:
(1) Hold alive and/or collect up to 50 black-capped chickadees per year in the form of eggs, nestlings, and/or adults for testing and analysis (total will not exceed 50).
(2) Hold alive and/or collect up to 10 adult red-breasted nuthatches per year for testing and analysis.
(3) Hold alive and/or collect up to 10 adult boreal chickadees per year for testing and analysis.
(4) Collect up to 20 adult northwestern crows per year for testing and analysis.

2. Population genetics of migratory birds.
Location: Countries outside the United States
Dates: January - December
Authorized Activities:
(1) Import or export lawfully obtained migratory bird samples (including carcasses, parts, feathers, blood or tissue samples,

[X] ADDITIONAL CONDITIONS AND AUTHORIZATIONS ALSO APPLY

12. REPORTING REQUIREMENTS

You must submit an annual to your Regional Migratory Bird Permit Office report each year, even if you had no activity.

ISSUED BY

TITLE
PERMIT SPECIALIST, MIGRATORY BIRD PERMIT OFFICE - REGION 7

DATE
04/08/2015

DNA, nests or eggs) for genetic analyses. As indicated in Condition D, additional authorization is required to import or export samples of bald eagles, golden eagles, threatened or endangered species or species listed under CITES.
(2) Samples will be stored dry or in a stable storage buffer.
(3) Samples originating from countries that have experienced an outbreak of the H5N1 strain of avian influenza will be treated to inactivate any live viruses by one of the following methods:
(a) heating at 60 degrees C for 30 minutes, or
(b) heating at 56 degrees C for 3 hours, and/or
(c) immersion in ethanol.

3. Monitoring nests of waterbirds
Location: State of Alaska
Dates: May - July
Project Leader: John Pearce
Authorized Activities: Authorized to conduct standard nest searching and monitoring activities for nests of waterbird species (swans, ducks, geese, and loons) as defined in the USGS Standard Operating Procedure "Monitoring Nests of Waterbirds".

4. Breeding ecology of Kittlitz's murrelets, marbled murrelets, and black-legged kittiwakes
Kittliz's and marbled murrelets
Locations: Icy Bay, Glacier Bay, Cook Inlet, Prince William Sound, Agattu, Atka, Adak, Unalaska, Kodiak, Port Heiden, Port Moller, Kachemak Bay, and Yakutat.
Black-legged kittiwakes:
Location: Prince William Sound
Dates of activities: May 2013 - October 2016
Project Leaders: John Piatt
Authorized Activities for each year:
(1) Capture birds and attach no more than thirty (30) adult Kittlitz's and thirty (30) Marbled murrelets 6.1 g satellite transmitter per year using non-absorbable sutures, for three year totals of 90 birds per species.
(2) Lethally collect up to thirty (30) black-legged kittiwakes per year for a 3 year total of 90 black-legged kittiwakes.

5. Distribution, movements, demography, and contaminants exposure in loons and grebes.
Location: Various locations of Alaska's North Slope and on the Seward Peninsula.
Dates: June 2013 - September 2016
Project leader: Joel Schmutz
Authorized Activities:
(1) Capture no more than 15 yellow-billed loons to obtain blood samples, feather samples, fat biopsies, and to implant 65-gram PTT satellite transmitters in each bird.
(2) Collect blood samples, feather samples, and fat biopsies from the following species:
a) up to 10 yellow-billed loons (in addition to YBLO in "8(1)" above);
b) up to 25 Pacific loons;
c) up to 40 red-throated loons; and
d) up to 10 red-necked grebes.

6. Seabirds as indicators of forage fish stocks and marine ecosystems in Alaska- Tufted Puffin chick diet and growth
Location: The Gulf of Alaska, including islands in the western and eastern Aleutian Archipelago, and islands throughout the central Gulf of Alaska
Dates: August 2013 - 2016
Project Leader: John Piatt
Authorized Activities: Screen over tufted puffin burrows (for under 2 hours) in order to collect prey items, and capture and process (measure and weigh) no more than two hundred and fifty (250) tufted puffin chicks per year for a 4 year total of up to 1000 chicks.

7. Habitat-use, growth rates, and survival of Hudsonian Godwit chicks
Location: Susitna Flats near Beluga
Dates: April 2014 - July 2018
Project Leaders: Rose Swift, John Pearce
Authorized Activities:
(1) Locate nests and visit daily until clutch is complete (3-4 days). Check nests every 2-3 days using binoculars and then daily at end of incubation to determine egg volume and hatch.
(2) Capture attach no more than 20 glue on VHF radios (0.6 g) to Hudsonian godwit chicks at time of hatch.
(2) Recapture briefly each radio-marked chicks every 3 days until 24 days of age (8 captures) to assess mass gain.
(3) Use radiotelemetry to locate chicks to conduct half-hour long behavioral observations on foraging habitat-use and track survival of chicks. Observations conducted with binoculars.

8. Vulnerability of Arctic-breeding insectivores to climate
Location: Colville River Delta
Dates: May 2015-August 2017
Project leaders: Dan Ruthrauff and Tom Fondell
Authorized activities:
(1) Collect up to 15 complete clutches a year (for a three-year total of 45 clutches) from Semipalmated Sandpipers and replace clutch with fake eggs. Hold clutches in chilled incubator to delay embryonic development. After 5 days, return eggs to original nest or a foster nest if original nest no longer active.
(2) Each year, glue VHF radios (<2 g) on up to 15 adult male Semipalmated Sandpipers from experimentally delayed nests. Affix VHF radios (.3 g) on 1-2 Semipalmated Sandpiper chicks from same nests.

9. Effects of parasite infections on gosling growth
Location: Yukon Delta National Wildlife Refuge, Colville River Delta, or Point Lonely
Dates: May 2015 - August 2017
Project leaders: Paul Flint and Courtney Amundson
Authorized activities:
(1) Capture 50 hatching Black Brant goslings per year (for a three-year total of 150 birds) for a captive rearing study lasting 35-40 days at a remote field site. Euthanize all goslings at end of study.

10. Effects of multi-scale environmental factors on the demography of birds in the boreal-arctic transition zone
Location: Livingston Creek and Neva Creek on the Seward Peninsula
Dates: May 2015 - August 2016
Project leaders: Colleen Handel and Steve Matsuoka (USGS), and Molly McDermott (UAF)
Authorized activities:
(1) Collect bolus samples from up to 20 nestlings (5 nests each) between ages 6- and 12-days post-hatch from Fox Sparrow, Lapland Longspur, Gray-cheeked Thrush, and Savannah Sparrow nests to determine insects fed to nestlings (total of up to 80 nestlings (and 20 nests) sampled per year and a two-year total of 160 birds (and 40 nests).
(2) Collect fecal samples from an additional 15 nests of all four species (60 nests/year and 120 nests for a two-year total)
(3) Multiple visits to each nest to measure growth rates of all four species.

11. Migratory Connectivity Project
Location: Colville River Delta
Dates: June - July, 2015 Only
Project leaders: Dan Ruthrauff and Joel Schmutz
Authorized activities:
(1) Capture up to 10 adult Black-bellied Plovers and 10 adult Ruddy Turnstones. Attach one 3.4-gram GPS-Argos PTT transmitter to each bird using a modified Rappole-Tipton attachment. Attachments will be constructed with a weak link to enable the transmitter to be shed once the radio is no longer functional.
(2) Capture up to 10 Pacific Loons and implant one 65-gram Argos PTT satellite transmitter in each bird.

E. Authority is granted to collect no more than 2 specimens (including eggs) of any species of migratory bird, except bald and golden eagles, threatened or endangered species, or the following species of concern: trumpeter swan, emperor goose, American peregrine falcon, Queen Charlotte goshawk, Eskimo curlew and Kittlitz's murrelet. Specimens will be prepared as museum study skins and housed in the Alaska Science Center's specimen collection room for scientific and educational purposes. Collections may be done by the following individuals: Paul Flint, Tom Fondell, Craig Ely, Colleen Handel, Lisa Pajot, John Pearce, John Reed, Dan Ruthrauff, Jerry Hupp, Joel Schmutz, Sandra Talbot, Lee Tibbitts, David Ward, Brandt Meixell, Andrew Ramey, Caroline Van Hemert, Rachel Richardson, Brian Uher-Koch, Steve Matsuoka, Molly McDermott, and Sarah Sonsthagen.

F. Permittee must have written authority from the Alaska Department of Fish and Game, Juneau, Alaska, before exercising any of the authorities granted by this permit.

G. This permit does not authorize the trespass on Native Corporation lands or villages, or any other private or public lands; contact the land owner for permission to access their land. Authorization must be obtained from the U.S. Fish and Wildlife Service prior to any collections on National Wildlife Refuge lands.

H. You are authorized to salvage dead migratory birds (except species listed as threatened or endangered under the Endangered Species Act). Any dead bald eagle or golden eagle salvaged must be reported within 48 hours to the National Eagle Repository at (303) 287-2110 and to the migratory bird permit issuing office at 907-786-3693. The Repository will provide directions for shipment of these specimens.

For a list of threatened and endangered species in your state, visit the U.S. Fish and Wildlife Service's (USFWS) Threatened and Endangered Species System (TESS) at: http://www.fws.gov/endangered.

I. You are authorized to salvage abandoned (unoccupied) migratory bird nests and nonviable eggs outside the nesting season, except for nests and eggs of bald eagles or golden eagles, or species listed as threatened or endangered under the Endangered Species Act.

J. You may not salvage and must immediately report to U.S. Fish and Wildlife Service Office of Law Enforcement any dead or injured migratory birds that you encounter that appear to have been poisoned, shot, electrocuted, have collided with industrial power generation equipment, or were otherwise killed or injured as the result of potential criminal activity. See FWS OLE contact information below.

K. You are authorized to import and export specimens of the migratory birds authorized above, including carcasses, nests, eggs, parts, blood and/or tissues. Additional authorization is required to import and export bald eagles, golden eagles, threatened and endangered species, and species listed under CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora).

L. All wildlife must be imported and exported through a wildlife designated port of entry/exit unless you have obtained a separate exception to designated port permit from the USFWS Office of Law Enforcement.

M. You must notify the USFWS Wildlife Inspector at the port of import or export **at least 3 days (72 hours) prior to import or export**. See the attached Standard Conditions for Migratory Bird Import/Export Permits for procedures specific to your activity.

N. You must declare your specimens to USFWS using USFWS Declaration for Importation or Exportation of Fish or Wildlife (Form 3-177; http://www.fws.gov/le/ImpExp/faqs.htm).

O. Any person who is
(1) employed by or under contract to you for the activities specified in this permit, or
(2) otherwise designated a subpermittee by you in writing, may exercise the authority of this permit.

P. You and any subpermittees must comply with the attached Standard Conditions for Federal Migratory Bird Scientific Collecting Permits and Migratory Bird Import/Export Permits. **These standard conditions are a continuation of your permit conditions *and must remain with your permit.***

For suspected illegal activity, immediately contact USFWS Law Enforcement at: 907-786-3693 or 800-858-7621

CHAPTER 4. GENERAL CONCLUSION

My research on the arthropod and songbird communities occurring in tundra-shrub ecotones in northwestern Alaska provides insights into likely patterns of short-term change as shrubs continue to expand in tundra ecosystems across the Arctic. Analysis of pitfall and sweep-net samples of arthropods collected during June and July of 2015 and 2016 showed heterogeneity among arthropod families in their associations with shrubs, but several groups were positively associated with willows (*Salix* spp.). DNA analysis of nestling fecal sacs revealed key prey items that could be targeted in future research on phenological mismatch. I also found patterns of diet diversity and flexibility that may help songbirds cope with projected fluctuations in the abundance and temporal availability of arthropod prey.

Although shrub expansion is occurring across the Arctic, the spatial extent and rate of change of different shrub species are site-specific (Myers-Smith et al. 2011, Elmendorf et al. 2012). Because willow, birch (*Betula* spp.), alder (*Alnus* spp.), and ericaceous shrubs (Ericaceae) offer different resources to herbivores and pollinators, I predict that differential increases in these shrub taxa are affecting Arctic food webs in different ways. All tall shrub species provide greater biomass of vegetation for herbivores than does tundra vegetation (Shaver and Chapin 1991), but willow is more palatable than birch or ericaceous shrubs (Mulder 1999). In Chapter 2, I provided evidence from model-selection analyses that overall abundance and biomass of arthropods increase with shrub cover, particularly tall willow species. Analysis of pitfall and sweep-net samples revealed that abundance of most major families of arthropods, especially herbivores, was positively associated with cover of tall willow. Abundance of most, but not all, pollinators was positively associated with cover of ericaceous shrubs, and species in this group had the highest predicted abundances at intermediate levels of tall willow cover. Ericaceous flowers and

willow catkins are both insect-pollinated (although some willows also use wind pollination) whereas birch and alder are not (Kevan 1972, Lundgren and Olesen 2005). Abundance of parasitoids was strongly associated with willow cover, and these responses, like those of herbivores, were mostly positive-linear or positive-curvilinear. Responses of predators were more heterogeneous, but few taxa of any trophic group exhibited a negative response to willow cover. Exceptions were herbivorous planthoppers (Cicadellidae) and leafhoppers (Delphacidae), which are known to feed on graminoids.

Consistent with model-selection results for individual arthropod families, results from ordination analyses indicated that willow cover and height, but not any measures of birch or ericaceous shrubs, were associated with significant changes in arthropod community composition. Based on these findings, I predict that in areas where willow is expanding most rapidly, such as western Canada and Arctic Russia (Myers-Smith et al. 2011), composition of the arthropod community is shifting dramatically and that most groups, particularly parasitoids and herbivores, are increasing in abundance.

While my research found generally positive impacts of tall willow shrubs on arthropods, in many regions other species of shrubs are expanding more rapidly. For instance, remote-sensing work has noted that the shrub species expanding the most in Alaska is mountain alder (*Alnus viridis* ssp. *crispa*) (Sturm et al. 2001, Tape et al. 2006), and tundra-warming experiments on Alaska's North Slope have shown dramatic increases in dwarf birch (*Betula nana*) (Bret-Harte et al. 2001). Increases in alder and birch, both wind-pollinated shrubs, may have a negative impact on pollinators. However, because birch is preferred by more herbivores than alder (Southwood 1961, MacLean and Jensen 1985, Mulder 1999), an increase in birch may benefit herbivores whereas an increase in alder may not be associated with such a benefit. In my study I

found few strong relationships with birch cover, but I did not have many observations of birch cover above 40% so my ability to forecast responses of arthropods to high birch cover is limited.

Vertebrate insectivores may benefit from increases in arthropod biomass with shrub expansion. To investigate trophic interactions between arthropods and songbird nestlings, I used next-generation sequencing of fecal samples from the Lapland Longspur (*Calcarius lapponicus*), American Tree Sparrow (*Spizelloides arborea*), Golden-crowned Sparrow (*Zonotrichia atricapilla*), Savannah Sparrow (*Passerculus sandwichensis*), and Gray-cheeked Thrush (*Catharus minimus*). The most important prey I identified were dance flies (Empididae), caterpillars (Lepidoptera larvae), and sawflies (Tenthredinidae; Chapter 3). Abundance of all 3 groups had a positive or positive curvilinear relationship with cover of tall willows (Chapter 2), indicating that increases in shrubs may benefit songbirds temporarily, but beyond 50-60% cover there may be declines in availability of these key prey items. These non-linear relationships could signify a potentially important effect of patch size as shrub thickets expand and become more homogenous. The edges of shrub thickets are often composed of a several-meter-wide band of mixed shrubs and tundra vegetation, but the center of the shrub thicket is often >60% shrub cover (Figure 4.1). In areas where shrub patches are small and narrow, an increase in shrub cover may create more edge area that benefits much of the arthropod community and the songbirds that depend on them for food. However, in large shrub patches, expansion may create proportionally more interior that exceeds >60% cover and is less suitable foraging habitat for birds.

These deciduous shrubs also provide nesting habitat more suitable for some birds, such as the Gray-cheeked Thrush (Boelman et al. 2015, Thompson et al. 2016) and support higher densities of nesting passerines (Sokolov et al. 2012), suggesting that some birds may benefit from increased habitat as well as increased food availability. Other species, such as the Lapland

Longspur, are less tolerant of shrubs and are expected to decline as a result of habitat loss (Thompson et al. 2016).

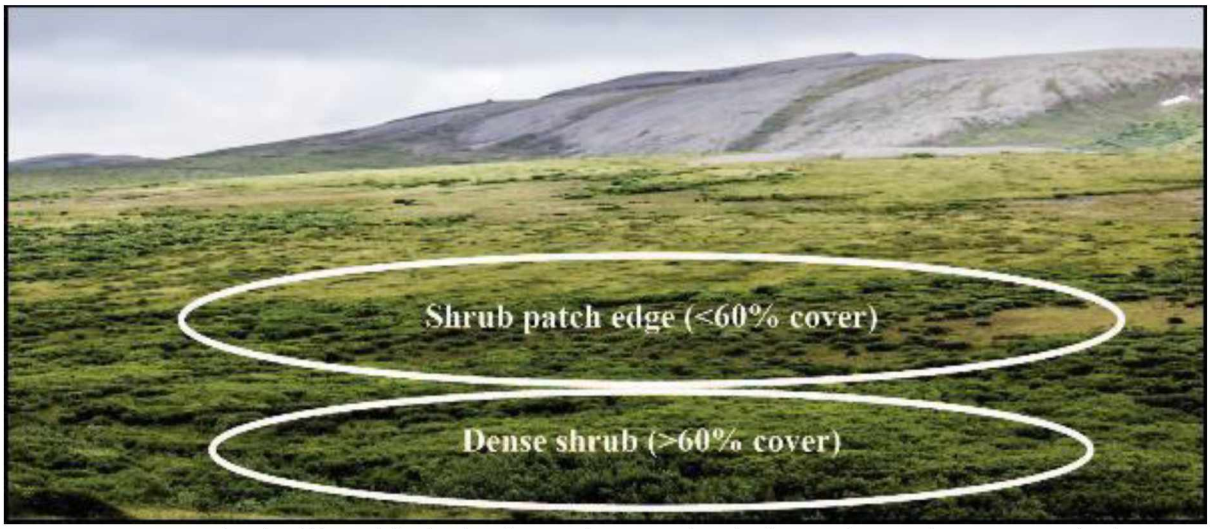

Figure 4.1 A typical willow-birch shrub patch around a drainage in northwestern Alaska. Center of the patch tends to be highly dense shrubs exceeding 60% cover, whereas surrounding edge areas are composed of interspersed shrubs and tundra vegetation. Photograph by Kaitlyn Wilson.

Nestling diets were highly diverse and varied spatially, indicating a great deal of flexibility in diet (Chapter 3). Despite this spatial variation in diet composition, I identified a few key prey items that birds may prefer regardless of availability. Key prey items were available throughout the breeding season, and the most frequently consumed arthropod family, dance flies, was available late in the season, potentially protecting these birds from negative effects of trophic mismatch. High dietary diversity may allow birds to adjust to the changes in food supply that are expected under continued climate change (Høye and Forchhammer 2008, Tulp and Schekkerman 2008).

I uncovered potentially important trophic interactions between plants, arthropods, and migratory songbird nestlings. Shrub patches supported greater abundance and diversity of arthropods, particularly herbivorous taxa, than found in tundra vegetation. Rapidly increasing

populations of herbivorous insects, if not controlled by predatory arthropods or some other mechanism, could cause significant damage to plants. Such increased insect damage has been observed in Subarctic Russia across the habitat gradient from tundra to shrub to forest (Kozlov et al. 2015). Increased insect herbivory has also been linked to past warming events in North America (Blois et al. 2013, Labandeira and Currano 2013). Songbirds exert some level of control of herbivorous insects, particularly when feeding nestlings. Thus, the net intensity of herbivory on plants would depend on songbird density and the relative frequency of predaceous and herbivorous arthropods in songbird diet. I observed that nestlings were fed herbivorous insects in a slightly greater proportion relative to their availability as measured by sweep-net samples; however, adult diets may have differed from those of their young. Thus, my findings suggest that generalist songbirds may provide at least a small benefit to plants in this system.

While there is a great deal of concern about how a changing climate may negatively impact the distribution and persistence of species, it is possible that shrub expansion may increase arthropod abundance and thereby provide some benefit to bird communities in northwestern Alaska. By studying existing differences between arthropod communities in tundra and shrub thickets we hope to inform predictions of how arthropod abundance and food-web structure may change with continued shrub expansion, at least in the short term. Increased shrub cover was associated with increases in abundance and diversity of arthropods, particularly herbivores that are preferred prey for songbird nestlings, indicating that an increase in shrub height and cover may increase arthropod abundance and prey availability for migratory birds. Songbird nestling diets were diverse and highly variable, suggesting these birds will be able to adjust to changes in local food availability. If shrub expansion continues to be associated with higher abundance of arthropod prey, I predict that food availability will not be a limiting factor

for any migratory songbird populations; however, continued expansion of shrubs will result in direct loss of habitat for tundra-nesting birds that will ultimately affect their populations negatively. Some birds, particularly shrub-associated species, may benefit from both increased habitat and food availability.

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